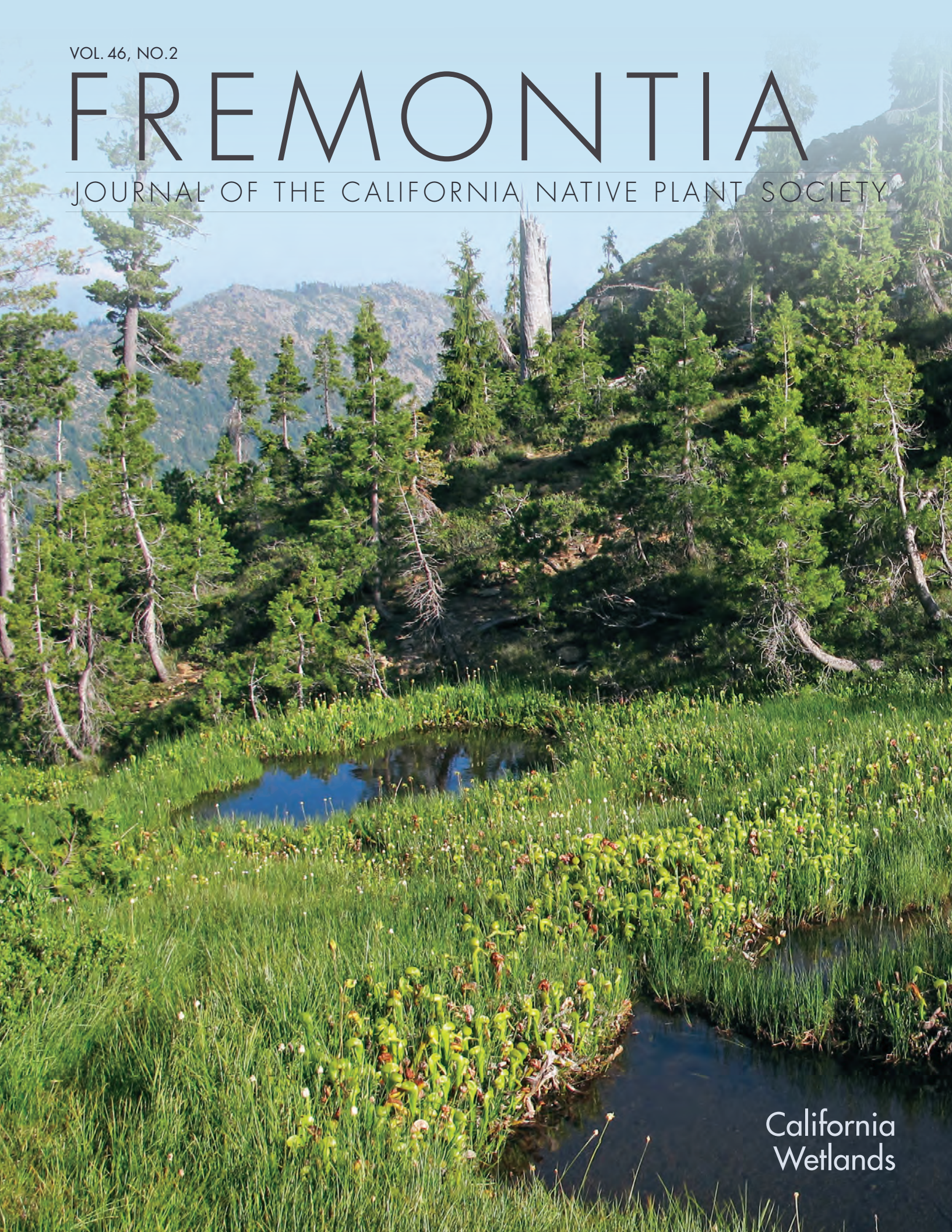


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CALIFORNIA
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Our mission is to conserve California's native plants and their natural habitats, and increase understanding, appreciation, and horticultural use of native plants.

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Cover: *Darlingtonia californica* fen
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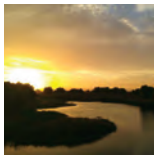
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INTRODUCTION TO THIS SPECIAL ISSUE ON CALIFORNIA WETLANDS

Gordon Leppig

Humboldt Bay is California's second largest estuary. Those on the North Coast who live and work around this large and alluring body of water are fortunate for the many ways to experience the beauty of its open water, salt marshes, and streamside wetlands. The bay's vast and charismatic wetland ecosystem is rich with a variety of fish, wildlife, and interesting plants.

While we may think of it as grand, its diversity, fecundity, and size were once much greater. Humboldt Bay has lost all but 900 of its original 9,000 acres of salt marsh habitat due to diking, draining, filling, and shoreline protection for transportation, agriculture, and the development of cities and industry.

In many ways, the fate of Humboldt Bay's wetlands mirrors that of all California wetlands. Western civilization has commonly viewed wetlands as useless wastelands, infeasible for agricultural, and too wet for development. Additionally, wetlands were considered breeding grounds for mosquitos, vermin, and disease. Consequently, what have we done to our wetlands? Cleared, filled, diked, and drained them.

While our wild rivers were once the heart and life-

blood of early civilizations because of the yearly bear-ings of irrigation water and nutrient-rich sediments, they are today often viewed as catastrophic flood-inducing and bank-eroding dangers. So what have we done to our rivers? We have armored their banks, put them in concrete channels, disconnected them from their floodplains, and generally dammed, straightened, and diverted them.

In the last half of the 20th century however, a deeper appreciation for wetlands has emerged. Beyond their numerous economic values, wetland and riparian habitats offer untold ecosystem services. People also flock to wetland and riparian areas to enjoy the open space, hike, swim, relax, and find spiritual replenishment and creative inspiration.

Despite their incalculable value, California and the rest of western North America continue to lose wetland acreage and values annually. Over the last 150 years, wetland filling or conversion for flood control, agriculture, navigation, transportation, and development has had the following results:

- California has lost approximately 90 percent of its original wetlands, a greater percentage than any other state.
- Approximately 90 percent of California's vernal

Above: Sunset over the salt marshes of Humboldt Bay's vast estuary.
Photo by Andrea Pickart.

pools and 80-90 percent of its original riparian forest are gone, and

- Almost every major river in the state has been dammed, diked, and substantially diverted for agricultural and domestic water use or flood control.

However, the joyful and motivating reality is that much valuable habitat remains and opportunities for restoration, enhancement, and expansion are vast. Articles in this issue cover most, but not all, of California's major wetland types. This issue explores their botanical diversity, explains their formation and ecological processes, reviews why they are valuable, how they are threatened, and how we can better protect, restore, enhance, and enjoy them.

The primary goal of this special Wetlands Issue of *Fremontia* is to educate and inspire. It focuses on the botanical beauty and values of California's vast and diverse wetlands and riparian habitats, which comprise numerous sensitive natural communities and host thousands of native plant species, rare and common, and a diverse assemblage of fish and wildlife.

Serving as a virtual ecological transect, these articles will take you from west-to-east and subtidal to subalpine. Beginning on the seafloor, the rocky intertidal and unusual eelgrass and surfgrass communities are brought to light by Rebecca Garwood and myself. Just above sea level, Michael Vasey and Peter Baye give a fascinating overview of the botanical diversity of California's tidal marshes. Mostly within earshot of the crashing surf, Mike van Hattem, Bill Maslach, and I present an overview of northern California's coastal fens and recent losses and successes in protecting and restoring these rare and localized habitat islands.

Moving further inland along our rivers, Bruce Orr and Amy Merrill explore disturbance-driven riparian forests. California's famously floriferous vernal pools are explored by Carol Witham et al. The transect ends with a review of the ecology and flora of our beautiful wet mountain meadows by Amy Merrill and Nicole Jurjavcic. In a broadly applicable study, Chelsea Teale and Eileen Hemphill-Haley introduce us to paleo-ecological techniques and how they can inform and guide wetland restoration projects. Lastly, Christian Braudrick et al. take us underground to explore the importance and connection of groundwater management and monitoring to wetland and riparian health.

In recent years, hundreds of acres of saltmarsh and estuarine habitat have been restored around Humboldt Bay and hundreds more acres of restoration are beginning soon. With this restoration, an extremely popular bay-wide trails system is being developed—enhancing public access to the bay and its adjacent rivers and wetlands. These trails are beginning to connect numerous communities in the Humboldt Bay region. This effort exemplifies the combined benefits of wetland restoration, ecosystem health, and enhanced human health and quality of life.

I hope you read on and become inspired to partner with your local CNPS chapter to protect, restore, enhance, and celebrate California's valuable and beautiful wetlands. I also hope you are inspired to invite children, parents, grandparents, friends, and neighbors to head for the nearest riverside trail, nature preserve, wildlife area, state park, or beach and explore all that these diverse habitats have to offer. Enjoy!

-Gordon Leppig: Gordon.Leppig@wildlife.ca.gov



Humboldt Bay owl's clover (*Castilleja ambigua* subsp. *humboldtiensis*) in a Humboldt Bay tidal marsh slough restored by the City of Arcata. Photo by Andrea Pickart.



BEYOND PLANTS: WETLANDS FOR WILDLIFE

Jennifer Olson & Gordon Leppig

As well as being botanical hotspots, wetlands and riparian areas offer vital habitats for a large assemblage of wildlife species—from the common to the rare. Fifty percent of federally listed animals and 28 percent of plants depend on wetland habitats (Niering 1988). In the Pacific Coast Ecoregion, 60 percent of amphibian species, 16 percent of reptiles, 34 percent of birds, and 12 percent of mammals are considered obligate riparian species (Kelsey and West 1998). In addition to breeding and rearing areas, wetlands and riparian corridors are important migration and dispersal routes for both aquatic and terrestrial wildlife.

Above (clockwise from top left): Mexican free-tailed bats (*Tadarida brasiliensis*) foraging at dusk, Yolo Bypass CDFW Wildlife Area. Photo by Gordon Leppig.

The state endangered willow flycatcher (*Empidonax traillii*), caught in a mist-net by CDFW staff at the Eel River Wildlife Area, Humboldt County. Photo by Jennifer Olson.

The California red-legged frog (*Rana draytonii*), an obligate wetland species, is the California State Frog, California's largest native frog, and federally listed as Threatened. Photo by Michael van Hattem.

In reality, most non-marine wildlife rely on riparian and wetland habitats to some degree. These systems are extremely productive and also a food source produced by the copious swarms of aquatic insects such as stoneflies, caddisflies, and mayflies. Willows (*Salix* spp.), a dominant component of many wetland and riparian habitats, are insect pollinated, thus attracting an entire different suite of flying insects—which are important prey for birds, bats, and more. Here we give a brief overview of the importance of wetland and riparian habitats to birds, bats, and amphibians.

BIRDS

Ask any birder for the best place to spot a variety of “good” songbirds, and they’ll probably point you to the nearest willow patch, marsh, or swamp. It’s well known that wetland and riparian habitats support a disproportionate number of bird species compared to their footprint on the landscape, especially in the arid west (Knopf and Samson 1994). California wetlands are a vital part of the Pacific Flyway, a major bird migration corridor of the western Americas. As such,

wetland and riparian areas provide exceptional habitat for hundreds of species of migratory waterfowl, shorebirds, and riparian songbirds, and attract more than 1.5 million ducks and 750,000 geese annually.

Wetlands also support a large number of California Species of Special Concern (SSC). SSC is a California Department of Fish and Wildlife designation given to wildlife species with declining populations, limited ranges, and/or continuing threats making them vulnerable to extinction. Though neither state nor federally listed, the goal for species with this designation is to halt or reverse their decline by addressing habitat conservation early enough to secure long-term viability. Of the 63 bird taxa currently designated SSC, 27 species (43 percent) primarily utilize wetland habitats and another 11 species (17 percent) are riparian forest inhabitants (Shuford and Gardali 2008).

Two SSCs, the yellow warbler (*Setophaga petechia*) and yellow-breasted chat (*Icteria virens*), are riparian obligate species that have experienced population declines due to habitat loss. Recovery of yellow warblers requires restoration of dynamic riparian systems resulting in a complex matrix of both early successional (young willow thickets) and structurally mature vegetation comprised of herbaceous, shrub, and forest canopy layers. Similarly, yellow-breasted chats are strongly tied to riparian habitats, but prefer early successional/shrubby understory vegetation for breeding. The greatest factor in the decline of the state endangered willow flycatcher (*Empidonax traillii*), is the extensive loss, fragmentation, and modification of riparian breeding habitats. Likewise, wetland loss is the principal threat to the state threatened greater sandhill crane (*Grus canadensis tabida*).

BATS

If you've spent time at night or dusk near rivers, lakes, or wetlands, it's likely you have noticed bats foraging for insects produced by these habitats. Bats disproportionately rely upon wetland and riparian habitats because of their rich food resources, open water, and appropriate roosting habitat for certain species. Bats are declining across North America and globally, due to many factors, but habitat loss is a big one. Until recently, bat conservation in California has been poorly addressed, and even today it remains sporadic. Consequently, habitat loss and other threats have resulted in 12 of California's 25 bat species being currently designated as SSC.

Population declines of species such as the cave

myotis (*Myotis velifer*) and the western red bat (*Lasiurus blossevillei*) are correlated with the loss of cottonwood (*Populus* spp.) and sycamore (*Platanus racemosa*) riparian forests (Pierson et al. 2006). Riparian restoration, particularly the recruitment of mature cottonwood and western sycamore forests and the reinstatement of natural flood regimes, would significantly benefit the western red bat, and generally, wetland and riparian restoration and expansion will greatly assist in the recovery of California's diverse bat fauna.

AMPHIBIANS

Most amphibians, such as frogs and salamanders, lay eggs in surface waters and have aquatic larvae requiring a wetland or stream to complete their life cycle. Thus, California's wetlands, streams, floodplains, and adjacent uplands are essential habitats for the vast majority of California's amphibian species. California has 45 amphibian SSC, the vast majority of which are reliant on wetlands and streams for all or a portion of their life history. Amphibians are undergoing a global collapse, and on a regional and state-wide scale numerous amphibian species are declining as well (Lannoo 2005, Wake and Vrendenburg 2008). For instance, half of the Sierra Nevada and Cascade's 29 native amphibian species are at risk of extinction, and though their threats are many and complex, habitat loss and fragmentation is one of the primary reasons for their decline (California Department of Fish and Game 2007).

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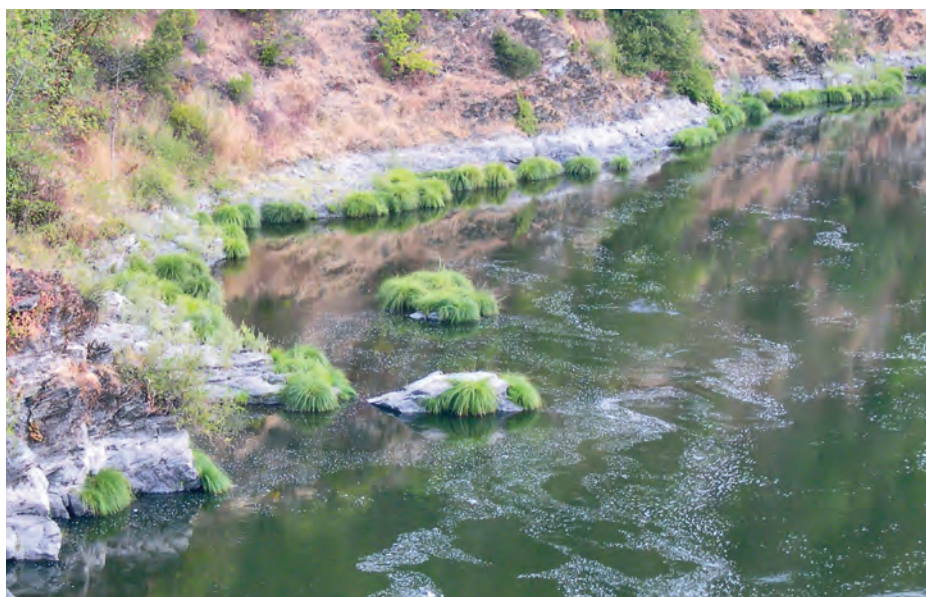
GETTING THE EDGE ON SEDGES

Gordon Leppig

Sedges (*Carex*), in the Cyperaceae, are a large and ecologically important group of perennial grass-like plants known for their affinity for wetlands. Virtually every wetland type in California—swamps, wet meadows, tidal marshes, lake margins—have at least one typically dominant sedge. Fens and wet serpentine sites often have the most diversity, with up to six or more species. More than half of California’s sedges are classified as obligate wetland plants (almost always found in wetlands) or facultative wetland plants (usually found in wetlands) (Lichvar et al. 2012). Though, there are more than a few dry grassland and forest species, such as the forest-dwelling wonder-woman sedge (*C. gynodynamia*) and stick sedge (*C. multicaulis*). Sedges can also dominate rocky subalpine habitats.

With almost 500 species, *Carex* is the largest plant genus in North America, and its 138 native and five introduced species also makes it California’s most speciose genus. Milkvetches (*Astragalus*) and wild buckwheat (*Eriogonum*), with dozens of rare local varieties and subspecies, have more taxa in California. But, unlike these genera, which exemplify our narrow endemics, most California sedges are widely distributed. The majority of California sedges occur throughout the U.S. mountain west and into Canada, and many, like the rare green yellow sedge (*C. viridula*) are circumboreal.

Diversity increases with higher latitude and altitude. Only 40 *Carex* are documented across the entirety of our southern desert regions, while Mendocino County has nearly 60 species. Only ten sedges appear to be endemic to California and they are primarily upland and drier habitat species.



ABOVE: The torrent sedge (*C. nudata*), along the Klamath River, is a common and widespread sedge along major rivers and large high-energy streams where it forms large dominant tufts on gravel bars and rocky banks. Photo by Gordon Leppig.

RIGHT: The green yellow sedge (*C. viridula*), at Big Lagoon Bog in Humboldt County, prefers fens, and sandy, acidic wetlands. This circumboreal species occurs across North America, but California has only eight documented occurrences in five counties. It has not been seen in Mendocino County since 1909. Photo by Gordon Leppig.





Bristle-stalked sedge (*C. leptalea*) is one of the rarest sedges in California, with eight known occurrences. Paradoxically, it is the most widely distributed sedge in North America. Seen here leaning on the fruits of yellow-eyed grass (*Sisyrinchium californica*). Photo by Gordon Leppig.

When a dominant component of the vegetation, sedges are an environmental keystone. Edible fruits are food for songbirds and waterfowl, and dense foliage offers songbirds nesting habitat and is forage for numerous mammals. Extensive rhizome and root systems bind soils and prevent streambank and shoreline erosion.

Riparian swards of white root sedge (*Carex barbarae*) once covered the Great Central Valley. Clonal patches were tended by Native American tribes for their long strong rhizomes used in basketry. This resource was traded across large distances (Stevens 2004). With wetland and riparian conversion in the Great Central Valley these once-common sedges have experienced a significant decline.

More than a quarter of our sedges (39 species) have a CNPS California Rare Plant Rank, and about half are wetland species. Livid sedge (*C. livida*) has not been seen in a Mendocino County sphagnum fen since 1866 and is presumed extirpated, while Tompkin's sedge (*C. tompkinsii*) is state listed as rare.

Even widespread species can be rare. The fen-dwelling bristle-stalked sedge (*C. leptalea*) is the most widely distributed sedge in North America, occurring in almost every state and across Canada, yet California has only eight known occurrences, three of which have not been located in over 75 years. Another was discovered in 2018 by CNPS botanist Alison Colwell.

Many sedges are rare because they have a narrow water chemistry preference and a hydrologic (soil moisture) regime tolerance—such as amount, duration, and timing of inundation (Wilson et al. 2014). The combination of hydrology and specific water chemistry parameters, such as pH and mineral content, helps explain why many rare sedges in California are strongly associated with fens or fen-like habitats. Examples include Buxbaum's sedge (*C. buxbaumii*), mud sedge (*C. limosa*), and the green yellow sedge (*C. viridula*). This same narrow wetland habitat preference also appears to hold true for the related Cyperaceous beaked-rushes (*Rhynchospora*). California has four beaked-rush species—all rare and obligate wetlands species.

Sedges have a well-earned reputation as being notoriously difficult to identify. This is because of their vast diversity, many superficially similar-looking species, and the numerous minute characteristics that make field identification challenging—and microscopic examination essential. Difficulty with identification has often lead to sedges being overlooked during plant surveys (and, in my opinion), under-appreciated. Sedges are clearly a group that many botanists could know better.

Fortunately for the *Carex* curious, sedge workshops are regularly offered by CNPS, the Friends of the Chico Herbarium, and others. Also, the *Field Guide to the Sedges of the Pacific Northwest, Second Edition* is an excellent reference (Wilson et al. 2014). It does not cover every sedge in California, but most sedges occurring in central and northern California are found in this beautiful field guide.

Finally, sedges can make a welcome and low-maintenance addition to many native plant gardens and landscaping projects. Growing them is a great way to get to know them. Consult Calscape.org or your local CNPS chapter for suitable native sedges to propagate in your area.

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SEAGRASSES: CALIFORNIA'S MARINE WILDFLOWERS

GORDON LEPPIG & REBECCA GARWOOD

From alpine lakes and wet mountain meadows, vernal pools to desert oases, California's wetland habitats are famously diverse, intrinsically beautiful, and hold a magnetic draw for botanists and plant lovers. Yet, if there were one California wetland habitat, indeed, one vast area of the state generally overlooked and under-appreciated—a botanical wonderland where most plant enthusiasts don't go looking for wildflowers—it's our marine environment. But here too, in the briny depths of California's thousand mile shoreline, from the high intertidal zone to 15 meters below the surface of the sea, are native plants hidden in plain sight.

On the ocean floor, surrounding our off-shore islands, along California's entire rocky intertidal coast, and in the tidal mudflats of our coastal bays and estuaries, lays a small and fascinating assortment of marine flowering plants known broadly as the seagrasses. Though masquerading as, and often mistaken for seaweed (algae), seagrasses are a highly unusual group of angiosperms found only in marine environments.

While one could amass an entire library on California's subalpine and alpine flora, our ultra-low-elevation flora is poorly studied and often overlooked. This is because most seagrass beds are difficult to access, requiring

either swimming, scuba diving, or boating to get to them. With a low tide, sturdy waiters or rubber boots for tidepooling or crossing deep mudflats are essential, but prepare to get wet no matter what.

While the global vascular plant flora includes almost 300,000 flowering plant species, and California alone has approximately 6,500 native plant taxa, there are only about 60 marine flowering plant species worldwide, and California is graced with only five truly marine species.

All of California's seagrasses are in the *Zosteraceae*—the Eelgrass family. Of these, three are in the genus *Zostera*: the eelgrasses (*Z. marina*, *Z. pacifica*), both natives, and the introduced *Z. japonica*. Our other two marine wildflowers are in the genus *Phyllospadix* (*P. torreyi* and *P. scouleri*), commonly called surfgrasses. Only one other California plant species comes close to acting like a seagrass—*Ruppia maritima*, a ditch-grass in the family *Ruppiaceae*. This species often forms large, spaghetti-like, filamentous mats higher up in estuaries and coastal streams in slow brackish waters—but it is not fully marine.

What sets seagrasses apart from the many salt tolerant halophytes that inhabit California's coastal salt marshes and desert/arid habitats? Seagrasses are strictly marine endemics, only occurring in intertidal and subtidal habitats where they are submersed in seawater or highly saline brackish water. Whereas halo-

Above: Surfgrass (*Phyllospadix scouleri*) in tidepools south of Trinidad, Humboldt County. Photograph by Gordon Leppig.

phytes are terrestrial plants adapted to grow in salt-rich soils and salt-laden air.

Almost exclusively rhizomatous perennials, seagrasses reproduce sexually through seeds and asexually through horizontal rhizomes. In shallow soft-bottomed seafloors, seagrasses can form vast rhizomatous clonal or semi-clonal meadows covering huge areas. And as such, similar to coral reefs, these meadows provide a complex ecosystem structure that is utilized by hundreds of other marine species for food, hiding, resting, rearing young, and foraging. Furthermore, these meadows can persist for millennia. A clonal meadow of the Mediterranean seagrass (*Posidonia oceanica*) is shown to be more than 4,000 years old and molecular techniques indicate that a Baltic Sea *Z. marina* clone is over 3,000 years old (Duarte 2002).

Like true grasses, seagrass flowers are reduced only to reproductive parts and are barely visible to the naked eye. Without showy petals and sepals, flowers are aligned in rows, surreptitiously tucked into flap-like straps hidden in their leaves, and completely inconspicuous. Eelgrasses are monocious, i.e., having female and male flowers on the same plant, while surfgrasses are dioecious, with entirely separate female and male plants. While flowers are inconspicuous, ripe fruits, though small achenes, are much more visible. Fruits, shoots, and rhizomes can disperse long distances via ocean currents but fruit consumption by waterfowl can result in long distance dispersal. Since seagrasses are a staple of the herbivorous tropical manatees and dugongs, grazers of this size have a profound influence on seagrass ecology, abundance, and global distribution.

Seagrasses occur in coastal habitats nearly world-wide. However, they are absent from Antarctica and only barely test the Arctic waters because the scraping of shoreline ice-scour prevents their establishment or persistence. The greatest abundance and diversity of seagrasses occurs in the middle and south latitudes of the west Pacific Ocean (Southeast Asia). The Indian Ocean along with the western central Atlantic Ocean and the Caribbean Sea are also zones of diversity, while Australia is a seagrass diversity epicenter with 31 species—about half of all seagrass taxa (Green and Short 2003).

EELGRASS—ZOSTERA

Eelgrass occurs in many protected coastal waters, including bays and estuaries, along the California coast from the Smith River estuary near the Oregon border



2009 aerial photo of the North Bay of Humboldt Bay showing dendritic channels dissecting mud flats (greyish-white) and vast *Zostera marina* beds (green). The circular features are former oyster farming beds, where the eelgrass has only partially revegetated. Photo from Schlosser and Eicher (2012).

to San Diego Bay in the south. However, five bays—Humboldt, San Francisco, San Diego, Mission, and Tomales—support more than 80 percent of the state's eelgrass beds. Approximately 14,600 acres of eelgrass have been mapped state-wide, with Humboldt Bay having the largest single occurrence with 39 percent of the state's eelgrass acreage.

Eelgrasses are keystone species, meaning their intrinsic ecological importance is so foundational and complex that it helps drive and support the entire ecosystem where they occur. Eelgrass beds are vital nursery and rearing habitat for the recreationally and commercially important Dungeness crab, Pacific herring, and rockfishes. Pacific herring utilize eelgrass extensively as a spawning substrate in Humboldt, Tomales, and San Francisco bays. Herring are an important food source for many birds, mammals, invertebrates, and fish. Additionally, the recreationally important black brant feeds exclusively on eelgrass, requiring large meadows for feeding along the bird's annual migration route from Alaska to Baja California, Mexico. Thus eelgrass meadows support entire ecologically and commercially important food chains.

By far the most common and widely distributed eelgrass in California and globally is *Zostera marina*, which occurs along the length of the California and Pacific Northwest coast, as well as across the Pacific and on both sides of the Atlantic. This species is generally found in calm waters in bays, estuaries, and lagoons, and in some nearshore coastal areas. Its distribution is limited by local conditions, including water clarity, elevation, protection from wave action, currents and tidal



California Department of Fish and Wildlife Environmental Scientist James Ray monitoring *Zostera marina* beds in Humboldt Bay, Humboldt County. Photograph by Gordon Leppig.

dynamics, water salinity, and a soft-bottom substrate.

California's only other native eelgrass is *Z. pacifica*. This species has had a fraught taxonomic existence because of its vexing morphologic similarity to *Z. marina* and *Z. asiatica*. However, recent genetic work appears to confirm that *Z. pacifica* is indeed a legitimate species, distributed throughout Southern California's coastal bights from Santa Barbara to the Channel Islands. The distribution of *Z. pacifica* along the rest of California's coast is poorly understood, with information no doubt limited by its clandestine existence—often rooted five to 15 meters below the sea, necessitating scuba diving to study it.

In 2008, the introduced *Z. japonica* was discovered by California Department of Fish and Wildlife (CDFW) staff in the Eel River estuary, Humboldt County, and soon after, in Humboldt Bay. Its native range is from Russia to Vietnam, but is now found in estuaries from Northern California to British Columbia. Concerted efforts to eradicate it have been undertaken by CDFW and others in the past. Thus far, it does not appear to be aggressively invasive in California. *Z. japonica* typically grows at a slightly higher tidal elevation than *Z. marina*, impacting areas that would otherwise typically consist of bare mudflat. Recent surveys in Humboldt Bay and the Eel River estuary have not detected the documented occurrences of *Z. japonica*, giving renewed hope that it may still be possible to eradicate this species in California.

Total acreage of eelgrass meadows in California by location listed from north to south.

Area	Acreage	% of State Total
Humboldt Bay	5,646	39%
Tomaes Bay	1,288	9%
San Francisco Bay	2,790	19%
Mission Bay	979	7%
San Diego Bay	1,955	13%
Other Sites	1,977	13%
Total Acres	14,635	—

SURFGRASS—PHYLLOSPADIX

California's two surfgrass species span the western coastline from the southern tip of Baja California north to the Queen Charlotte Islands and the Alexander Archipelago of British Columbia and Alaska. Unlike other species of seagrass, which are typically submersed in protected areas with depositional substrates (sandy/silty bottoms), surfgrasses only occur on exposed, wave prone rocky shores. They are essentially an intertidal species strenuously attaching to rocks in order to withstand constant wave action and changing tides.

Both species of surfgrass occupy similar habitats, with *Phyllospadix torreyi* found slightly lower in the rocky intertidal zone than *P. scouleri*. The leaves of *P. torreyi* are rounded and wiry, generally less than 2mm

wide, and grow as long as 3 meters. In contrast, the leaves of *P. scouleri* are flat, shorter, and wider, with blade widths ranging from 2-4 mm and blade lengths up to one meter.

Surfgrasses form dense stands in rocky intertidal areas and have a variety of adaptations to help them survive in these high energy environments. Their fibrous rhizomes and rootstocks keep plants attached to rocks under constant wave-crashing disturbances. The crescent-shaped fruits have two arms with backward-facing bristles to enhance attachment to other host plants. Seedlings commonly rely on host plants for seed germination until rhizomes can form and attached to the rocks (Blanchette et al. 1999). Once successfully rooted, the new recruit may eventually crowd-out the older host plant.

Compared to *Z. marina*, relatively little is known about the ecology of surfgrasses. However, like all seagrasses, surfgrasses offer a variety of ecological benefits including nursery habitat for fishes and invertebrates like California spiny lobsters and food for herbivores like the Pacific green turtle. Mats of surfgrass also dampen the impacts of storms and waves on the surrounding environment. Surfgrasses shade tidepools during low tide events, helping to maintain cooler water temperatures. As detrital wrack washes up on the beach, surfgrasses also provide nutrients and habitat for foraging beach invertebrates, ultimately providing prey to shorebirds and nearshore sandy beach fishes.

Seagrass meadows, like many other state and global coastal ecosystems, face numerous threats. Twenty-nine percent of the known areal extent of seagrass meadows has disappeared since the late 1800s, with the rate of decline rapidly accelerating over the second half of the 20th century (Waycott et al. 2009). In California, over the past 150 years, the two greatest threats have been habitat loss and degraded water quality. Direct habitat loss has resulted from “land reclamation” in the form of filling shallow coastal waters for ports, including docks and piers, and extensive coastal development through placement of garbage dumps, airports, roads, and cities in estuaries. Beach nourishment projects, which replenish eroded and disappearing beaches with sand, are becoming more common in southern California, and can impact seagrass beds. Dredging and widening of shipping channels is another threat to seagrass beds.

Seagrasses require clear water to capture sunlight. The deeper they grow the clearer and cleaner the water must be, making them vulnerable to cloudy water and sediment inputs (Zimmerman 2006). Urban



Phyllospadix torreyi (left) and *P. scouleri* (right) at Baker Beach near Trinidad, Humboldt County. Photograph by Rebecca Garwood.



Pacific herring eggs on a *Zostera marina* blade. Pacific herring eggs are sticky when extruded and adhere in large masses to substrates such as rocks, seaweed, or eelgrass. These eggs are an important seasonal food source for migratory birds and numerous fish species. Photo by Rebecca Garwood.

stormwater and agricultural runoff causes increased nutrient loading and decreased light levels on the seafloor through eutrophication and algal blooms. Decreased water quality and massive sedimentation loads caused the collapse of San Francisco Bay’s commercial oyster industry more than 100 years ago, while also degrading its eelgrass beds. In comparison, Humboldt Bay still maintains a thriving and highly valued oyster [aquaculture] industry—by far the state’s



LEFT: The sea hare (*Phyllaplasia taylori*), a gastropod mollusk related to slugs and snails, on *Zostera marina* blades. *P. taylori* occurs from British Columbia to San Diego County and lives exclusively on *Z. marina*. Its size, shape and coloration are adapted for life on eelgrass blades, where they slowly feed on a diversity of epiphytes. Photo by California Department of Fish and Wildlife.



RIGHT: The Albion River estuary in central Mendocino County has approximately 30 acres of eelgrass, extending over 3 miles from the river's mouth. It is an unusual California example of a "drowned river valley" with saltwater extending 4-5 river miles inland. This location provides a rare opportunity to see extensive eelgrass beds, salt marsh, and redwood forest, all within a few feet of one another. Photo by Rebecca Garwood.

largest commercial oyster production, in addition to the states' most extensive eelgrass beds—due in large part to the bay's relatively clear, clean, and shallow waters.

Zostera marina meadows have declined 90 percent in the last century along the Atlantic coast of the United States and Europe (Bockelmann et al. 2013). This catastrophic decline is attributed to eelgrass wasting disease caused by a marine protist (*Labyrinthula zosterae*). The virulence of this disease can vary widely, with some *Z. marina* beds experiencing almost complete loss, while others remain unaffected. From 2007 to 2013, Morro Bay, San Luis Obispo County, lost 96 percent of its eelgrass meadows, over 329 acres. The exact cause of this loss is unclear, though eelgrass wasting disease is the suspected culprit. Since the decline, a series of eelgrass reestablishment efforts have been attempted in Morro Bay, many of which have failed or had limited success.

Rising sea levels combined with more frequent and more intense high-energy storms, both of which are anticipated by California climate models, could result in higher rates of coastal erosion, nearshore turbidity, sedimentation, and seagrass habitat loss. Ocean acidification, a result of greenhouse gas emissions, is also expected to have a profound effect on marine ecosys-

tems, with uncertain impacts on seagrasses. Moreover, seagrasses have been shown to buffer acidification in surrounding waters, highlighting the need to protect and restore these habitats in California as the world's oceans become increasingly acidified due atmospheric carbon absorption.

CONSERVATION AND FURTHER EXPLORATIONS

The Clean Water Act, California Environmental Quality Act, the California Coastal Act, and related laws in the 1970s have helped to improve the state's coastal water quality and management. Furthermore, the National Marine Fisheries Service, the U.S. Fish and Wildlife Service, and the CDFW have all designated eelgrass meadows as a sensitive habitat for protection and require mitigation for projects resulting in eelgrass loss (NOAA 2014). Additionally, as we write this, renewed federal efforts are under way to expand oil drilling off California's coast, which could impact our seagrass habitats in numerous ways.

Today, sea level rise and related changes to nearshore ocean conditions are one of the greatest challenges for maintaining seagrass populations in the state. Other climate-related threats include disease introduction or

Important ecological and economic benefits of seagrass beds (from Duarte 2002) include:

- Habitat for larval and juvenile fishes, invertebrates, waterfowl, shorebirds, and numerous endangered and commercially important species
- Food for coastal food webs
- Oxygenation of waters and sediments
- Atmospheric carbon sequestration
- Organic carbon export to adjacent ecosystems
- Trapping and cycling of nutrients
- Sediment stabilization
- Prevention of sediment resuspension
- Improvement of water transparency
- Wave energy attenuation
- Shoreline erosion protection

susceptibility and invasive species. How will estuarine ecosystems respond to sea level rise? One important aspect of local sea level rise adaptation planning is to ensure that eelgrass meadows and other estuarine habitats either have enough sediment to adjust their height to new higher water depths or have areas to migrate landward. If a principal sea level rise adaption strategy of state and local agencies is to harden our shorelines with levees, sheet piles, and rock armor, which do not allow for estuarine habitat to expand landward, then we are likely facing a scenario of significant loss of eelgrass meadows in the coming decades.

More scientific research and a greater understanding of seagrass ecology is essential to conservation and sea level rise adaptation planning. There are currently expanding worldwide efforts to map and monitor seagrass populations and document the status of seagrass resources and threats. For instance, CNPS and CDFW collaborate to map and describe the state's natural communities; however, marine habitats have not previously been included in the state's vegetation mapping and assessment efforts (Sawyer et al. 2009). Fortunately, for the past few years CNPS and CDFW have been working to accurately map the abundance and distribution of, and to better describe, these seagrass natural communities.

Exploring seagrass meadows is absolutely unlike any other botanical experience. Only among the seagrass can you exchange your interest in bryophytes and lichens for that of seaweeds and corals, and insects for crustaceans. Instead of encountering bears and

mountain lions, you are more apt to watch whales and sea lions. Among the seagrasses is the only place in California where you can bask in a vast meadow, tens or even hundreds of acres across, but comprised of only one native plant species—and not see a single weed. Only in these spectacular habitats can you botanize while gazing out off the edge of the continent to the most distant horizon—and virtually every species you behold is exotic, yet comfortingly native.

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NORTH COAST FENS: BIODIVERSITY HOTSPOTS OF GREAT BOTANICAL RICHNESS

Gordon Leppig, Michael van Hattem, & William Maslach

Fens are one of California's most unusual and diverse hydro-botanical hotspots. These wetlands form over the course of centuries or millennia, as a thick layer of peat develops. Peat is an organic soil type (Histosol) typically defined as being at least 40 centimeters thick, though California fens often have peat layers from 1-5 meters deep. Peat forms where cold groundwater sources result in perennially saturated, low oxygen conditions, which limits nutrient availability and inhibits microbial decomposition (Moore and Bellamy 1974).

These highly unusual growing conditions result in rare assemblages of plants (Leppig 2004). This is why

fens are the only California habitat where carnivorous plants commonly occur. The exception are the aqueous bladderworts (*Utricularia*), which also occur in lakes and other open water habitats. While the carnivorous California pitcher plant (*Darlingtonia californica*) occurs in the Klamath Mountains, North Coast Range fens, and Butterfly Valley in Plumas County, it also occurs in serpentine seeps and springs where its presence is related more to the unusual serpentine bedrock soil and water chemistry than to peat soils (Sawyer 1986).

Peat formation is strongly associated with peatmoss (*Sphagnum*) in arctic and alpine environments; however, in many regions, fens are primarily dominated and created by sedges (*Carex* spp.). Broadly known as a type of peatland, fens tend to form in concave depressions or on slopes with streams flowing through them (Crum 1992). Bogs, another peatland type, are disconnected

Above: With the addition of a 132-acre parcel in the fall of 2018, the Crescent City Marsh Wildlife Area in Del Norte County will include most of the wetlands and Sitka spruce (*Picea sitchensis*) forest in the lower center and left. Photo by Justin Garwood.



The largest population of the state and federally endangered western lily (*Lilium occidentale*) occurs in the Crescent City Marsh. Photo by Michael van Hattem.

from ground or surface water and are instead hydrated by precipitation only. By this definition, only fens occur in California—there are no true bogs. However, in this article, we use the local common names when referring to specific sites.

The Jepson Manual uses a diversity of overlapping terms when describing these habitat types, including: bog, fen, sphagnum swamp, sphagnum bog, boggy site, and peatland. In totality, these terms characterize oligotrophic (nutrient poor) peatlands, where the vegetation is either quaking (it shakes when you jump on it), or completely floating (undulating when you traverse it). In all cases this habitat is always saturated at some soil depth. Based upon differences in vegetation (*Sphagnum* produces acidic conditions) or bed-rock geology (limestone produces alkaline conditions), California fens can be acidic to alkaline, but many tend circum-neutral to alkaline (Leppig 2002; Wolf and Cooper 2015).

If vernal pools, the quintessential California wetland, are an artifact of California's Mediterranean-type climate, then fens are their ecological and floristic opposite. Fens occur in California despite, rather than because, of the Mediterranean-type climate. While vernal pools are dominated by rare, narrowly endemic annual plants, California fens are dominated by tufted or rhizomatous perennials and shrubs with a strong northern boreal or arctic affinity, such as species common throughout the western high mountains like marsh cinquefoil (*Comarum palustre*) and Labrador tea (*Rhododendron columbianum*), or species occurring along the coast to Alaska like Pacific reed grass (*Calamagrostis nutkaensis*).



Some of the most well-known and extensively studied fens on the North Coast.

NORTH COAST FENS: A SERIES OF HABITAT ISLANDS

The vast majority of California's fens are found in the Sierra Nevada, Klamath, and Cascade mountains. For the most part, the vegetation and ecology at these sites has been well described (Sikes et al. 2011; Wolf and Cooper 2015). However, the vegetation, ecology, and flora of many North Coast fens have not been extensively studied. From north to south, North Coast fens form a series of small, discrete, and well-dispersed wetlands from near the Oregon border south, historically, to San Francisco. Peat formation at most of these sites likely originated when rising seas inundated coastal areas over the past 6,000 years and remained relatively stationary (until recently) for years. For this reason, the boreal biogeographic affinity of these fens, current flora are expressions of a relict ancient (Pleistocene) flora.

Coastal fens, like other disjunct substrates such as limestone or serpentine, act as habitat islands, and thus



Big Lagoon Bog, in Humboldt County, with western azalea (*Rhododendron occidentale*), Labrador tea (*Rhododendron columbianum*), and Pacific reed grass (*Calamagrostis nutkaensis*) in the foreground and a Sitka spruce (*Picea sitchensis*) forest in the background. Photo by Gordon Leppig.

maintain aggregated and disjunct clusters of rare plants and unusual natural communities (Leppig 2004). The bogbean (*Menyanthes trifoliata*), is an excellent example of localized rarity and disjunct ecological significance. While common in the Sierra Nevada's wetlands and lake shores, it is rare on the North Coast, occurring almost exclusively in fens. Del Norte County has only two known bogbean occurrences. In Humboldt County, it is known from a small cluster of fens on McClellan Mountain, many of which were mined illegally for peat and destroyed. Mendocino County has only two occurrences, with only one on the coast. It appears undocumented in Sonoma County; Marin County has only one; and the most southern coastal occurrence was in San Francisco but was eliminated in the late 1800s.

CRESCENT CITY MARSH

The Crescent City Marsh is a 600-acre coastal wetland and Sitka spruce (*Picea sitchensis*) forest complex, of which 335 acres comprise the California Department of Fish and Wildlife's (CDFW) Crescent City Marsh Wildlife area. From afar, it looks like a typical coastal marsh dominated by slough sedge (*Carex obnupta*), cattail (*Typha latifolia*), and hard stem bulrush (*Schoenoplectus acutus*). Continue exploring and rare botanical treasures abound, including vanilla grass



Sphagnum sp. with sporophytes, big leaf rhododendron (*Rhododendron macrophyllum*), white beaked-rush (*Rhynchospora alba*), and Mendocino cypress (*Hesperocyparis pygmaea*) seedling at Sholars Bog. Photo by William Maslach.

(*Anthoxanthum nitens*), great burnet (*Sanguisorba officinalis*), Arctic starflower (*Trientalis arctica*), and an extensive population of bogbean. Unbeknown to CDFW when they acquired the marsh, it also holds the largest California population of the state and federally endangered western lily (*Lilium occidentale*).

The Crescent City Marsh is bounded by State Highway 101 and commercial development to the west, separating it from the beach. It is threatened by altered hydrology and diminished water quality from extensive residential and commercial development on its borders. For years, occluded culverts under Highway 101 draining the marsh raised its water levels and severely impacted the western lily (western lily bulbs need to dry out in the summer). CDFW and Caltrans are currently working to correct this drainage problem—and hopefully the western lily will respond favorably. In another successful CDFW and Caltrans joint venture, CDFW is adding approximately 90 acres of wetlands to the marsh, including an occurrence of western lily, and 40 acres of rare mature Sitka spruce forest on its edge.

BIG LAGOON BOG

Long known as an important plant area (IPA), Big Lagoon Bog is a three-acre fen and part of Humboldt County's Big Lagoon County Park. It occurs in the

brackish marsh-fresh water ecotone at Big Lagoon State Park, and as such, it has an unusual mix of typical saltmarsh plants like arrowgrass (*Triglochin maritima*) and silver hairgrass (*Deschampsia cespitosa*). Typical fen species include extensive mounds of *Sphagnum* moss with locally rare round-leaved sundew (*Drosera rotundifolia*). The bog club-moss (*Lycopodiella inundata*) which for decades appears to be just barely persisting, is one of only two populations in California. Other rare plants include the marsh pea (*Lathyrus palustris*), and extensive populations of Buxbaum's sedge (*Carex buxbaumii*) and the green yellow sedge (*C. viridula*). The bristle-stalked sedge (*C. leptalea*), one of California's rarest sedges, also occurs here.

New threats, both natural and anthropogenic, have arisen. Mountain heath grass (*Danthonia decumbens*), a perennial Eurasian invasive, was discovered in the bog in 1990 and has since become prevalent. On and off plans to build a nearby casino, with an on-site wastewater treatment system, is a potential threat to the site's hydrology and water quality. But the biggest threat is encroachment by woody vegetation. Consequently, with the support of the CNPS North Coast Chapter, Caltrans is funding woody vegetation removal at the bog. A graduate student and the chapter will be monitoring the responses of the plants. Fortunately, Big Lagoon Bog has little nearby development, is surrounded by Sitka spruce forest, and has plenty of room for upslope migration to adjust to higher sea levels or more saline conditions.

INGLENOOK FEN

Nestled in the Ten Miles Dunes of MacKerricher State Park and insulated from human activities, this central Mendocino coastal fen is isolated. Radio carbon dating of the peat indicates the fen is 4,000 to 6,000 years old. Its quaking mats are at least 30 feet deep—botanizing here feels like standing on the back of a sauntering woolly mammoth.

Ringed by a dense thicket of Hooker's willow (*Salix hookeriana*) and California wax myrtle (*Morella californica*), the open center is dominated by bogbean, Rocky Mountain pond-lily (*Nuphar polysepala*) and an impressive suite of sedges, including, Cusick's sedge (*Carex cusickii*), Sitka sedge (*Carex aquatilis* var. *dives*), star sedge (*Carex echinata* subsp. *phyllomanica*), woodrush sedge (*Carex luzulina*), and woolly sedge (*Carex pellita*). Plants with arctic affinities persist as relics of the last ice age, including marsh cinquefoil, round-leaved sundew, kneeling angelica (*Angelica genuflexa*), and Sierra



Big River Laguna dominated by a thick carpet of *Sphagnum* moss, with Labrador tea (*Rhododendron columbianum*), Cusick's sedge (*Carex cusickii*), and cat tails (*Typha latifolia*). Photo by Gordon Leppig.

bog rein-orchid (*Platanthera dilatata* var. *leucostachys*). The fringed corn-lily (*Veratrum fimbriatum*) and swamp harebell (*Campanula californica*) are locally endemic rare plants. The fen has the only Mendocino County occurrence of beaked spikerush (*Eleocharis rostellata*).

SHOLARS BOG

Two miles east of Fort Bragg, Sholars Bog occurs on one of a series of flat, uplifted marine terraces up to 500,000 years old. Nutrient-poor soil forms an impenetrable hardpan (podzol) that traps water on the surface like a swimming pool liner. A profile of the bog revealed a meter-thick layer of peat overlaying the mineral substrate of sandy clay. The famous stunted "pygmy forest" surrounding the site consists of Mendocino cypress (*Hesperocyparis pygmaea*) and Bolander pine (*Pinus contorta* subsp. *bolanderi*). Both trees comprise a Sensitive Natural Community currently being described and mapped by CDFW.

The College of the Redwoods currently owns the Sholars Bog, but the site is for sale and its fate is uncertain. CDFW, CNPS, and others are working to conserve the site. Fens in the Fort Bragg area are subjected to a litany of serious threats, including, ditching to drain these wetlands, off-road vehicles, trampling, dumping, vandalism, rare plant poaching, intentional introduction of exotic carnivorous plants, degraded

TABLE 1. CARNIVOROUS PLANTS NATIVE TO CALIFORNIA.

California has nine native carnivorous plants. All are considered obligate wetland plants and most are associated with acidic water, peatmoss (*Sphagnum* spp.), and boggy fen conditions. Bladderworts (*Utricularia* spp.) are aquatic and rooted or free-floating in deep water. Six of the nine native species have a CNPS California Rare Plant Rank. A small number of other exotic carnivorous species, including *Drosera* spp. and eastern pitcher plant (*Sarracenia*) have been intentionally introduced into North Coast fens, where some have persisted and could become invasive.

Scientific and common name	State Rank/ Rare Plant Rank
California pitcher-plant (<i>Darlingtonia californica</i>)	S4/4.2
English sundew (<i>Drosera anglica</i>)	S2/2B
Round-leaved sundew (<i>Drosera rotundifolia</i>)	—
Butterwort (<i>Pinguicula macroceras</i>)	S2/2B2
Flat-leaved bladderwort (<i>Utricularia intermedia</i>)	S3/2B2
Lesser bladderwort (<i>U. minor</i>)	S3/4.2
Cream-flowered bladderwort (<i>U. ochroleuca</i>)	S1/2B.2
Common bladderwort (<i>U. macrorhiza</i>)	—
Humped bladderwort (<i>U. gibba</i>)	—



Round-leaved sundew (*Drosera rotundifolia*). Photo by Gordon Leppig.

water quality, erosion, and extensive large scale development. State and local agencies, CNPS, and others are working to address these threats, but we clearly have our work cut out for us.

BIG RIVER LAGUNA

The Big River Laguna Fen occurs in Mendocino County, east of the town of Mendocino. California State Parks acquired it in the early 2000s, and its ecology and flora have yet to be fully explored, despite the fact that Willis Jepson explored here in 1936. For fen fanatics it is a fantastic floristic feature, like no other coastal fen. Big River Laguna is a poorly connected tributary stream whose confluence, eight miles from the Pacific, occurs where tidal influence terminates on the mainstem of Big River. Here lays a flooded C-shaped stream valley one and a half miles long and 200-500 feet wide blanketed with what is most likely, California's largest floating vegetation mat.

On massive quaking mats of sphagnum grow western azalea, deer fern (*Struthiopteris spicant*), cat-tail, Labrador tea, and extensive tussocks of Cusick's sedge (*Carex cusickii*). Botanical exploring is perilous here because the floating vegetation is so aqueous and pocked with hidden holes that falling through the

mat into the mucky deep is a constant hazard. This is one reason the site remains ripe for further botanical exploration.

BAY AREA FENS

South of Mendocino County, coastal fens are increasingly imperiled and degraded (or lost) due to urbanization, but the floras remain fascinating. The 27-acre Pitkin Marsh, near Forestville, for instance, is one of California's richest and most enigmatic rare plant hotspots. Its flora is so unusual it warranted a 90-page dissertation (Rubzoff 1953). Now owned by the Sonoma Land Trust, it is part of the massive, but much diminished, Laguna de Santa Rosa marsh complex in Sonoma County.

The state and federally endangered Pitkin Marsh Lily (*Lilium pardalinum* subsp. *pitkinense*) is nearly endemic to the Pitkin Marsh, as is the Pitkin marsh Indian paintbrush (*Castilleja uliginosa*). Beaked-rushes (*Rhynchospora*) are reliable fen indicators and Pitkin Marsh is perhaps the only place in California where three of our four species co-occur: the white beaked-rush (*R. alba*), California beaked-rush (*R. californica*), and the round-headed beaked-rush (*R. globularis*). The populations of California round-head beaked-rush are disjunct at



On the North Coast, the carnivorous and locally rare round-leaved sundew (*Drosera rotundifolia*) appears to be restricted to fens and Darlingtonia (*Darlingtonia californica*) seeps, where it can be common. Photo by Gordon Leppig.



An 11-acre fen, illegally mined for peat, is now slated for experimental restoration by replacing stockpiled peat and restoring its hydrology. Photo by CDFW.

least 1,000 kilometers from their closest Midwestern occurrence. In addition to overgrazing, other threats include a lowered water table from groundwater pumping, invasive species, adjacent development, and agriculture.

Marin County's Point Reyes National Seashore has a number of unusual fen or fen-like wetlands. Ledum Swamp, for instance, had California's southernmost occurrence of bristle-stalked sedge, last seen in 1943, while the California beaked-rush was last seen there in 1945. The site has since been over-grazed and degraded and its ability to support rare plants is uncertain. Other sites include quaking peat in the paleodunes near Bull Point and the headwater swamp of Kehoe Creek, which is now the most southern coastal occurrence of bogbean.

The long-since destroyed Mission Bay Fen in San Francisco, also known as Russ Gardens, is a lost botanical wonderland generally considered our southern-most coastal fen. Occurring on marshy sand flats west of Mission Bay, it may have been California's earliest recognized botanical hotspot. It was extensively collected by the 19th Century botanical pantheon: Kate Brandegee, Alice Eastwood, Henry Bolander, and Albert Kellogg. But it was Herman Behr who

aptly described its disjunct plants as "a speck of the Arctic flora" (Behr 1880).

The bogbean occurred there—its historical coastal southern terminus. The federally endangered marsh sandwort (*Arenaria paludicola*) was collected near this site. The Mission Bay Fen had cotton-grass (*Eriophorum gracile*), yellow pond-lily, grape-fern (likely *Sceptridium multifidum*), and Sierra bog rein-orchid. By the 1890s, the burgeoning City of San Francisco "reclaimed" the area. For morbid curiosity, the first author explored the site (southeast corner of Sixth and Harrison streets) in 2001, and—no surprise—found a gas station and no use for a plant press.

Besides the usual wetland threats of invasive species, development impacts, and climate change, all fens are threatened by declining groundwater. So maintaining both surface water inputs and stable groundwater levels are key to their survival. The loss of natural disturbance regimes, such as wildfire or grazing, is also a major threat. But in many cases, to effectively protect them, they first need to be identified.

For decades a series of rare fens in the back-woods of Humboldt County were illegally mined for peat, which was sold for marijuana cultivation. Three fens, totaling more than 19 acres, were destroyed. We will



The bogbean (*Menyanthes trifoliata*) common in the Sierra Nevada, but rare on the North Coast and diagnostic of fen habitats. Photo by Gordon Leppig.



Corn-lily (*Veratrum fimbriatum*) and deer fern (*Struthiopteris spicant*) in Inglenook Fen. Photo by William Maslach.

never know their botanical richness. In 2013, a legal settlement was reached with the peat miner, which included attempting restoration of an 11-acre fen by replacing stockpiled peat and repairing its heavily altered hydrology. Two remaining fens are now protected, one as a result of this settlement and the other for compensatory mitigation. This illegal peat mining occurred because we were not diligent in identifying these sites and promoting their conservation.

Therefore, we recommend more focused rare plant surveys of coastal wetlands, especially those that appear to be fens or have *Sphagnum* or Labrador tea, which are reliable coastal fen indicators. These coastal fens could be perfect for CNPS rare plant treasure hunts. We are confident that with more botanists exploring coastal wetlands, the odds of rediscovering historical rare plant populations, or of finding new rare or disjunct populations, is exceedingly high. We also find that the vast majority of coastal fens represent sensitive natural communities yet to be described and mapped. To better understand these habitats and assist with their conservation, CDFW and CNPS should redouble our efforts to conduct vegetation studies in these rare and fascinating wetlands.

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THE EXTRAORDINARY DIVERSITY OF NATIVE TIDAL MARSH PLANTS IN CALIFORNIA

Michael Vasey & Peter Baye

California tidal marshes are assumed to be relatively low in plant species diversity and dominated by specialized species that tolerate extremes of physiological stress from harsh, intermittently waterlogged, high saline environments. Recently formed or disturbed salt marshes are often dominated by a few pioneer species, like the ubiquitous pickleweed (*Salicornia* [*Sarcocornia*] *pacifica*), which has strong colonizing ability as well as outstanding tolerance for highly saline soils. But determined exploration of the California tidal marsh flora reveals a surprising richness of native plants species.

The unexpected species diversity of California tidal marshes is revealed by expanding searches in different parts of the California coast, in higher tidal zones, along saline to brackish or fresh-brackish zones, in dis-

tinctive marsh soil types, and especially in relict mature marshes linked to vegetated upland habitats by riparian and seasonal wetlands. California tidal marsh plant species richness is also revealed by exploring out of the way places at unusual times of the year. For example, the ephemeral spring and summer annual flora can be discovered in the transition zone. Another rich source of information is documentation of occurrences by early botanical explorers before losses of diversity caused by habitat degradation due to diking, draining, filling, and reclamation. Finally, thoughtful reconstruction of biogeographical affinities of tidal marsh species and recent geological history of the Pacific coast lends additional context to these observations.

ORIGINS OF MODERN CALIFORNIA TIDAL MARSH FLORA

The diversity of modern tidal marshes in California is related to both past and current environmental processes. We often focus on the modern coastal envi-

Above: Tidal salt marsh at China Camp State Park, Marin County, one of the historic remnants of the San Francisco Estuary and now part of the San Francisco Bay National Estuarine Research Reserve (SF Bay NERR). Photo by Michael Vasey.

ronment as key to understanding contemporary tidal marsh plant biogeography, understandably because it is what is most readily available for study. However, the deeper prehistoric patterns of California tidal marsh species diversity are scarcely known. Ancestral populations of salt-tolerant tidal marsh species evolved during periods of post-glacial migrations. During climate oscillations in previous Pleistocene glaciations, low sea levels resulted in extensive coastal estuaries (Jacobs et al. 2004). During the Holocene epoch, beginning approximately 10,000 thousand years ago, these antecedent estuaries and their tidal marsh flora were most likely distributed more continuously along an exposed broad coastal plain. This prehistoric environment is now submerged offshore as sea levels rose and rugged coastal bluffs came to dominate the California coast (Masters and Aiello 2007).

Our modern coastline has existed for only about 4,000 years and historic tidal marsh floras represent relatively recent recombinations of these ancient, fragmented estuarine plant communities. The rapid, early post-glacial rise of sea level—more than 10 times the rate of the last several millenia—forced accelerated landward migration of this flora for over 6,000 years as migrating marshes became established. California’s current tidal marsh flora began to stabilize between 4,000-2,000 years ago. These later marshes, formed during slow rates of sea-level rise, are now revealed by sediment cores that document late Holocene climate and vegetation history seen in the stratigraphy of pollen, seeds, diatoms, foraminifera, tsunami sediment deposits, and elemental isotopes (Malamud-Roam et al. 2007).

EARLY CALIFORNIA BOTANICAL RECORDS REVEAL LOST TIDAL PLANT MARSH DIVERSITY

Botanical exploration of California tidal marshes in the mid- to late-19th century was sporadic, but the scattered plant collections with labels indicating “salt marsh” habitats provide a tantalizing window into unexpected plant diversity before widespread destruction took place from the mid-19th century to mid-20th century. Willis Jepson (1911) described species known today primarily from vernal pools, such as flatface downingia (*Downingia pulchella*), as “abundant and of rank growth in salt marshes near Alvarado [San Francisco Bay, near modern Union City]” and smooth popcorn flower (*Plagiobothrys glaber*) was noted from the “margin of salt marshes.” Katharine Brandegee, J.B.



Johnny nip (*Castilleja ambigua* subsp. *ambigua*), a rare, hemiparasitic annual shown here in the high salt marsh zone of an ancient sandy wash-over fan behind Limantour Spit, Point Reyes National Seashore. Photo by Peter Baye.



Pacific pickleweed (*Salicornia pacifica*), a dominant perennial of high tidal marsh plains in California, and flowering Pacific salt marsh dodder (*Cuscuta pacifica*), an annual stem parasite often associated with pickleweed. Photo by Peter Baye.



Downingia pulchella occurs in brackish nontidal marshes at San Francisco Estuary historical locations of tidal marsh transition zones severed from the bay by dikes. Photo by Peter Baye.



The Sears Point tidal wetland restoration encompasses nearly 1,000 acres of former diked bay lands. It is an innovative project of the Sonoma Land Trust that uses mounds, artificial pannes, and transition levees to protect the shoreline from wind-wave erosion and act as nuclei for colonization by salt marsh vegetation; e.g., Pacific cordgrass (*Spartina foliosa*). This is one of several large-scale tidal wetland restoration projects surrounding San Pablo Bay in Marin, Sonoma, and Napa counties. The “moss”-like mats shown here among other species colonizing this specially-constructed transition zone are the uncommon dwarf spikerush (*Eleocharis parvula*). Photo by Michael Vasey.

Davy, and E.L. Greene, reported many plant species from “salt marshes” and “borders of salt marshes” that are known today from brackish to freshwater marshes farther up the salinity gradient of the San Francisco Bay, now known more broadly as the San Francisco Estuary (SFE), such as iris leaf rush (*Juncus xiphioides*), annual coast plantain (*Plantago elongata*), and sea milkwort (*Lysimachia* [*Glaux*] *maritima*). The locations of these rare 19th century San Francisco Bay collections are today dominated by widespread marsh plants and bordered by artificial levees that lack complex shoreline features. For example, the Suisun marsh aster (*Symphotrichum lentum*), with a common name suggestive of local endemism in brackish reaches of the SFE, is now extirpated from Central and South San Francisco Bay tidal marshes. Other historical salt marsh species were likely lost when their brackish above-tide transition zones were eliminated by agricultural and urban development.

HISTORIC LOSS AND DEGRADATION OF TIDAL MARSH

Tidal marshes are among the most threatened ecosystems in California, especially those in Southern and Central California as well as those in the SFE. During the reclamation-dominated eras of the 19th and 20th centuries, the SFE—with the largest extent of tidal wetlands in California—lost more than 90 percent of

its estuarine marshes (Atwater et al. 1979). Due to loss and fragmentation, several endemic species became threatened while range restrictions and habitat isolation have resulted in a decline of genetic diversity.

Threats to remnant tidal marshes have also been exacerbated by a few problematic invasive, non-native plant species, such as the dense-flowered cord grass (*Spartina densiflora*), which now dominates much of the saltmarsh habitat in Humboldt Bay. In the late 20th century, environmental laws designed to protect water quality and federal- and state-listed threatened and endangered species led to a movement to restore tidal marshes. Current awareness of the ecological importance and ecosystem services provided by tidal marshes has further incentivized tidal marsh restoration in the early 21st century. Today, for example, thousands of acres of former tidal marsh habitat in the SFE are undergoing restoration.

AN OVERVIEW OF TIDAL MARSHES IN CALIFORNIA

A number of tidal marsh studies in California have been published (e.g., MacDonald and Barbour 1974, MacDonald 1977, Grewell et al. 2007, Callaway et al. 2012, Peinado et al. 2012, Peinado et al. 2016) and all suggest a similar biogeographic pattern for California’s marsh plants. California occurs at the crossroads of two major floristic assemblages—

NORTH COAST TIDAL MARSHES

With the exception of Humboldt Bay—a large tidal lagoon formed in the lee of barrier beaches (sand spits)—tidal marshes in Northern California occur in drowned river valleys. These narrow estuaries range from full salinity near the mouths to brackish and freshwater tidal marshes extending miles upstream. Streams with mouths sheltered from direct exposure to Pacific waves (e.g., Ten Mile River, Albion River, Big River, and Garcia River) form relatively stable tidal inlets with complex perennial estuarine marshes extending upstream. Streams with mouths directly exposed to the Pacific swell tend to form seasonal inlets that close off in spring and summer when freshwater flows diminish. This results in the impoundment of fresh water lagoons above tide levels. The Navarro River, Gualala River, and Mattole River form such seasonal estuaries with tidal marshes fringing their banks. These maritime estuarine marshes occupy valleys that funnel cool, foggy air masses upstream.

The composition of North Coast tidal marshes is typically dominated by species of rhizomatous, creeping graminoids; e.g., Lyngbye's sedge (*Carex lyngbyei*) in the intertidal zone, slough sedge (*Carex obnupta*) in the high tide transition zone, and Baltic rush (*Juncus balticus* subsp. *ater*). Native grasses are typically caespitose (tufted) or tightly rhizomatous, e.g., coast hairgrass (*Deschampsia cespitosa* subsp. *holciformis*), Bering hair grass (*Deschampsia cespitosa* subsp. *beringensis*), alkali grass (*Puccinellia nutkaensis*), and brackish-tolerant ecotypes of red fescue (*Festuca rubra*). North Coast tidal brackish marshes also support forbs with wide boreal distributions. Sea milkwort (*Lysimachia* [*Glaux*] *maritima*), sea arrowgrass (*Triglochin maritima*), and sea-side plantain (*Plantago maritima*) are as much at home in Northern California tidal marshes as they are on North Atlantic coasts of Europe and North America. Pacific silverweed (*Potentilla anserina* subsp. *pacifica*) and cow clover (*Trifolium wormskioldii*) are other tidal marsh species with ranges extending from the Pacific Northwest down through the Central Coast.

The tidal salt marshes of the North Coast also include many genera and species that occur along the arid-summer/wet-winter Mediterranean estuaries of the Central and South Coast, including pickleweed (*Salicornia pacifica*), saltgrass (*Distichlis spicata*), fleshy Jaumea (*Jaumea carnosa*), and sea-lavender (*Limonium californicum*). They are distinguished by the absence of some typical dominants of this southern region, such as alkali-heath (*Frankenia salina*), and uncommon



The rare annual California endemic, Humboldt Bay owl's clover (*Castilleja ambigua* subsp. *humboldtensis*) has fleshy leaves and rose-purple bract tips. Found here at the Garcia River Estuary, Mendocino County (southern limit of the typical form). Photo by Peter Baye.



Big River estuary found along the coast of Mendocino County. Relatively pristine tidally influenced salt and brackish marshes can still be found along the northern coast of California dominated by native wetland species with associated native submerged aquatic vegetation. Photo by Peter Baye.

Central and South coast subshrub Chenopod species, such as the sea-blites and salt-bushes. Also, unlike the South Coast, vegetation of tidal marshes along the North Coast typically occurs in mosaics rather than distinct zonation patterns.

Rare plants in North Coast tidal marshes include the beautiful Humboldt Bay owl's clover (*Castilleja ambigua* subsp. *humboldtensis*). This annual hemiparasite grows in low vegetation of high brackish or salt marshes at its type locality (Humboldt Bay). Small populations also occur locally at the mouths of Big River and Garcia River, Mendocino County. An atypical southern form, with bracts tipped white instead of rose-purple, occurs as far south as Tomales Bay, Marin County. The northern subspecies of salt marsh bird's-beak (*Chloropyron maritimum* subsp. *palustre*) has large populations in tidal marshes at Humboldt Bay and it nears its northern limit in southern Oregon.

SOUTH AND CENTRAL COAST TIDAL MARSHES

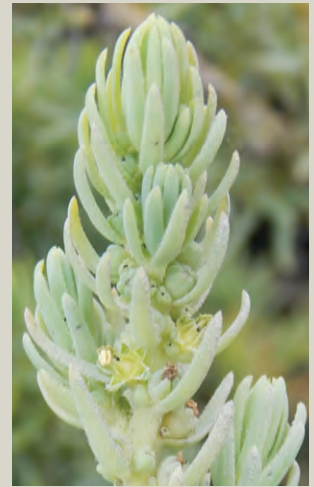
South and Central Coast tidal marshes are relatively small, although some—like tidal marshes characteristic of Elkhorn Slough—were probably once more extensive. These estuaries are less exposed to high-energy Pacific waves, and are often associated with lagoons behind moderately stable tidal inlets separated from the ocean by barrier beaches. Signature species of South Coast tidal salt marshes include shoregrass (*Distichlis* [*Monanthochloe*] *littoralis*) and saltwort (*Batis maritima*). Parish's pickleweed (*Arthrocnemum subterminale*) is a characteristic high salt marsh forb in this region including other chenopods such as saltwort and annual pickleweeds or glassworts (including the widespread annual pickleweed and southern Bigelow's pickleweed, which both occur within the Pacific cordgrass zone).

Zonation patterns are often well-developed in saline South Coast tidal marshes. The high salt marsh zone is typically dominated by halophytes prevalent in Central Coast salt marshes, including pickleweed and a number of other species such as fleshy jaumea and sea arrowgrass. The highest spring tide zone is characterized by saline playa-like flats that host species, such as Parish's pickleweed and shoregrass. Where seasonal lagoons close off from tides during the summer, salt marshes undergo wider fluctuations in salinity, ranging from hypersaline to brackish. Important salt-tolerant grasses of South Coast tidal marshes include saltgrass and Pacific cordgrass (*Spartina foliosa*). Saltgrass grows in brackish as well as salt marshes, primarily in upper intertidal zones and terrestrial transition zones. It also tolerates periods of non-tidal hydrology in estuaries that are seasonally choked off or closed. Pacific cordgrass, however, is limited to mid- to low-intertidal salt marsh zones with year-round full tidal range. Pacific cordgrass is prominent in Northern Baja and South Coast tidal marshes but absent in Central Coast estuaries until reaching the SFE where it is the dominant mid- to low-marsh species.

Rare plants of South Coast salt marshes include two annuals that occupy sparsely vegetated high marsh zones: salt marsh bird's-beak (*Chloropyron maritimum* subsp. *maritimum*), marginally distinct from its northern subspecies in morphology and ecology; and the spring annual Coulter's smooth goldfields (*Lasthenia glabrata* subsp. *coulteri*). The most extreme kind of rarity—resurrection from presumed extinction—is manifested by a coarse perennial, the Ventura marsh milkvetch (*Astragalus pycnostachyus* var. *lanosissimus*),

which is endemic to high salt marsh and adjacent dune and riparian vegetation of Ventura and Los Angeles counties. It was revived from an exhumed buried seed bank and is now the focus of recovery. It is slightly distinct (more wooly shoots and leaves) from a Central and North Coast counterpart, the marsh milkvetch (*Astragalus pycnostachyus* var. *pycnostachyus*), and both probably represent fragmented vestiges of more widespread, early Holocene populations. Morro Bay hosts the last natural site for the federally-listed endangered California seablite

(*Suaeda californica*). Estuary seablite (*Suaeda esteroa*) is another Chenopod salt marsh subshrub like Parish's and Pacific pickleweeds, but it is a rare plant native to high salt marsh and estuarine beaches from Santa Barbara to Baja California.



California seablite (*Suaeda californica*) is similar to other salt-tolerant wetland species in the Chenopodiaceae (e.g., *Salicornia* and *Arthrocnemum*) that are prominent in Southern California tidal marshes. A 13-year-old experimental pilot reintroduction project in San Francisco Bay has plants that have flowered and produced viable seed, and reproduced at least two generations. Photo by Peter Baye.



Morro Bay tidal marsh. In the foreground is the federally-listed endangered California seablite (*Suaeda californica*), which grows in a wide range of tidally influenced wetlands, sheltered beaches, sandy high salt marsh berms, and low bluffs in Morro Bay. Photo by Peter Baye.

LOWER SAN FRANCISCO ESTUARY (SFE) TIDAL MARSHES

Spanning 1,600 miles of tidally influenced waters, the present SFE tidal marshes represent a mere vestige of their former glory. SFE waters range from hyper-saline in south San Francisco Bay to fresh water in the Delta and upstream tributaries draining into major embayments like San Pablo Bay. Today, a network of levees, lowlands reclaimed from former marshes, urban communities built on filled marshes, and relatively low-diversity post-Gold Rush tidal marshes dominate the SFE landscape. Still embedded in this former marsh matrix are significant relict, prehistoric tidal marshes that retain their original peats, sediments, and terrestrial connections. These historic remnants now represent hot spots of endemism and diversity in the SFE.

In the lower SFE, the tidal marsh flora of central and south San Francisco Bay supports nearly all species found in Central Coast tidal marshes to the south (e.g., Elkhorn Slough), and also most North Coast tidal marshes. Some high salt marsh plants associated with beach and dune margins, like California salt-bush (*Atriplex californica*), are now extirpated in the SF Bay. Similarly, the endangered California sea-blite (*Suaeda californica*), native to Morro Bay, had a disjunct population in the San Francisco Bay, which was extirpated by the 1960s. One important SFE endemic that is still common on margins of tidal creeks and in transition zones is the San Francisco gumplant (*Grindelia stricta* var. *angustifolia*). Besides bringing splashes of golden color to dull green marsh expanses, this short-lived shrubby species provides cover, breeding, and roosting habitat for many salt marsh bird species.

An important contribution to tidal marsh richness in the lower SFE comes from formerly neighboring terrestrial or riparian vegetation in the uppermost transition zones. (Baye et al. 2000). Here, salinity is reduced to brackish ranges by rain-fall or near-surface groundwater discharge. Riparian sedge meadow grasslands, often mixed with saltgrass and alkali-heath, extended to the upper edge of tidal brackish and salt marsh and can include several graminoids such as field sedge (*Carex praegracilis*), basket sedge (*Carex barbarae*), Baltic rush (*Juncus balticus* subsp. *ater*), brown-headed rush (*Juncus phaeocephalus*), iris leaf rush (*Juncus xiphioides*), and the wide-ranging creeping wild-rye (*Elymus triticoides*) and related hybrids. Disturbed tidal marsh borders host annual Fitch's spikeweed (*Centromadia fitchii*) in the northeastern SFE and common spikeweed (*Centromadia pungens*) along the South Coast. A number

of other native annual species also occupied this zone, such as jonny nip (*Castilleja ambigua*) and saltmarsh bird's beak (*Chloropyron maritimum* subsp. *palustre*).

It is the marginal habitats that formerly linked tidal wetlands to adjacent uplands that have largely disappeared due to the great human-caused transformation of the lower SFE and its terrestrial surroundings. Important viable remnants can still be found in a few special places, offering tantalizing glimpses of a rich past, and these isolated populations could serve as sources for future restoration activity. Recovering high levels of native plant diversity will require landward migration of the tidal marsh shoreline into conserved lowlands as sea level rises, converting them to new high tidal marsh zones. Only a few key subregions still support the potential for tidal marsh migration.



Sarah Ferner, education coordinator at the SF Bay National Estuarine Research Reserve, pauses to examine San Francisco gumplant (*Grindelia stricta* var. *angustifolia*), an ecologically important member of the Asteraceae endemic to the San Francisco Estuary. Photo by Michael Vasey.

UPPER SAN FRANCISCO ESTUARY (SFE) TIDAL MARSHES

Suisun Marsh and portions of the upper reaches of San Pablo Bay support brackish tidal marsh systems dominated by California tule (*Schoenoplectus californicus*), hard stemmed tule (*Schoenoplectus acutus* var. *occidentalis*), broadleaf cattail (*Typha latifolia*), southern cattail (*Typha domingensis*), narrowleaf cattail (*Typha angustifolia*), threesquare bulrush (*Schoenoplectus americanus*), alkali-bulrush (*Bolboschoenus maritimus*), Baltic rush, salt-grass, and diverse assemblages of native brackish-tolerant forbs and grasses that extend into fresh-water tidal marshes of the Delta. In the historic freshwater Delta, several species of shrubs and trees were also present such as button willow (*Cephalanthus occidentalis*) and willow (*Salix lasiolepis*), as well as floating aquatic species (e.g. *Stuckenia* spp.).

Boreal North Coast elements of both salt and brackish marshes extend to the upper SFE, at or near their southern limits. For example, alkali grass (*Puccinellia*

nutkaensis) reaches the San Francisco Bay, where a robust form was previously treated as a distinct species (*Puccinellia grandis*). Lyngbye's sedge (*Carex lyngbyei*) apparently reaches south to Tomales Bay on the outer coast, and inland to the Napa River estuary and Suisun Marsh, where it is morphologically similar to Sitka sedge (*Carex aquatilis* var. *dives*) in the Delta.

Some of the rarest plants also occur in the Suisun Marsh. The federally listed endangered Suisun thistle (*Cirsium hydrophilum* var. *hydrophilum*) is a local endemic concentrated at Rush Ranch Open Space Preserve (a component of the SF Bay National Estuarine Research Reserve). Another federally listed species is the hemiparasitic soft bird's beak (*Chloropyron molle* subsp. *molle*). Like vernal pool annuals, population sizes and floral displays of soft bird's beak fluctuate from year to year, but tend to re-occupy approximately the same locations over time. As in the lower SFE, the Suisun Marsh was extensively altered, primarily by diking and ultimate conversion to managed seasonal wetlands for duck hunting clubs. Remnant tidal wetlands such as Rush Ranch and Browns Island, near the eastern edge of Suisun Bay, have much higher plant species richness today than the lower SFE (Vasey et al. 2012), probably because of their more extensive brackish to fresh water conditions.

While tidal wetlands in the lower SFE and Suisun Marsh have been extensively impacted by human modification, transformation of the Delta has been even more profound. It is estimated that less than two percent of historic tidal wetlands remain (Whipple et al. 2012). Most of these historic wetlands occur as small islands within large river channels that are diked on both sides for water control and agricultural purposes. These remnant islands, such as at Sand Mound Slough, can present remarkable diversity (Vasey et al. 2012) including such species as marsh skullcap (*Scutellaria galericulata*), marsh cinquefoil (*Comarum* [*Potentilla*] *palustre*), and rough bugleweed (*Lycopus asper*), rare in California but more widespread in post-glacial fresh-water wetlands in other states. The western central Delta is also characterized by a unique plant community first recognized by Herbert Mason as "willow-lady fern scrub" (Whipple et al. 2012). These species and assemblages are likely remnants of vast freshwater marshes that once characterized the Central Valley during the Pleistocene (Jacobs 2004).



The Suisun thistle (*Cirsium hydrophilum*) is a local endemic in the Suisun Marsh. Currently, about 90 percent of its known population is found in a 1,050-acre remnant tidal wetland at Rush Ranch Open Space Preserve, a property managed by the Solano Land Trust and designated as one of two components of the San Francisco Bay National Estuarine Research Reserve. The Suisun Thistle is a federally-listed endangered species. Photo by Michael Vasey.

Boreal and Mediterranean. A boreal-type climate (Boreal) tidal marsh flora extends from Alaska through British Columbia, south to Northern California. Tidal marshes in this region are dominated by sedges, rushes, caespitose (tufted) grasses, and a number of distinctive salt-tolerant herbaceous genera that are widespread in tidal wetlands found in circumboreal regions of the Northern Hemisphere. In these regions, precipitation tends to exceed evaporation and estuaries are more brackish than fully saline. A Mediterranean-type flora dominates subtropical tidal marshes from Central and Southern California south to Central Baja. Tidal marshes in this region are more saline or hypersaline and dominated by succulent, salt tolerant species in families such as the goosefoots (Chenopodiaceae) and composites (Asteraceae) as well as specialized, salt-tolerant rhizomatous grasses. In this region, reduced rainfall and long, dry summers lead to evaporation exceeding precipitation.

Floristic elements of these two broad assemblages co-occur in various combinations along the California coast lending a distinctive flavor to California's tidal marshes. In addition, California's tidal marshes are characterized by several endemic California species (Californian) from genera such as bird's-beak (*Chloropyron*) and owl's clover (*Castilleja*). It is these Californian endemics that increase the richness of California's tidal marsh vegetation and that are the most at risk from further loss.

Tidal marshes in the SFE are the epitome of this blending of Boreal, Mediterranean, and uniquely Californian floristic elements. The number of acres of tidal marsh in the SFE, both historically and at present, dwarfs the rest of the California coast. Interestingly, in the SFE, these three elements are distributed in counter-intuitive patterns. Tidal marshes in the lower SFE (San Pablo Bay and San Francisco Bay), close to the cool and more moderate climate of the coast, are distinctively Mediterranean and dominated by species characteristic of Central and Southern California. Conversely, in the upper SFE (Suisun Bay and the Delta), where it is considerably hotter and drier, tidal marshes are dominated by Boreal floristic elements more characteristic of the North Coast. This juxtaposition, particularly in the Suisun Marsh, has nurtured a high concentration of endemics.

These counterintuitive distributional patterns are most likely created by the broad salinity gradient that is driven primarily by the Sacramento River and the San Joaquin River, which collectively drain about 40 percent of California. These fresh water flows

dominate the upper SFE, whereas the lower SFE is dominated by tidal pulses of saline ocean water that fills the lower SFE and pushes up the Carquinez Straight into Suisun Bay. In recent centuries, the salinity gradient results in fresh to brackish conditions in the upper SFE that are more suitable for species of Boreal affinities as opposed to saline to hyper-saline conditions in the lower SFE that favor Mediterranean ones.

REFLECTIONS

We have only recently begun to appreciate the lost and cryptic plant species richness of California tidal marshes. This flora, established in its contemporary setting during the past few thousand years, has done so during periods of slow and stable rates of sea-level rise after millennia of extreme fluctuations in the early- to mid-Holocene. Tidal marsh plants today face accelerated sea-level rise and rapid climate change. However, these species must also overcome human-built obstacles for land-ward, upslope migration and suspended sediment supplies impacted by profound drainage alteration and diversion.

These are major obstacles to otherwise resilient tidal marsh ecosystems and floras. At the edge of these human-modified estuaries, increased rates of sea-level rise and reduced sediment supply threaten to result in large-scale marsh drowning and erosion. These trends will be playing out in the face of more frequent, extreme floods and droughts, and competition from new invasive, non-native species. Numerous wildlife species are also at risk from these same factors. How



A doomed valley oak (*Quercus lobata*), originally established above highest tides, is now partly submerged by seawater at China Camp in the SFE. As sea levels rise, so must the vegetation at the edge of wetlands. Photo by Peter Baye.

can we conserve this remarkably rich California tidal marsh flora in the face of these formidable land use and water use challenges?

In our view, although there is no one clear answer, we see many promising signs of a potential solution now in the making. Tidal marsh habitat restoration is taking place up and down the coast, from Humboldt Bay to San Diego Bay. In the SFE, 30,000 acres of restoration have been initiated and another 30,000 are committed through nine Bay Area county tax initiatives. Endangered species recovery and experimental population relocation studies are now underway with species such as Ventura marsh milkvetch, California sea-blite, Suisun thistle, and soft bird's-beak. Major invasive plant species control efforts are being conducted. Living shorelines are being designed to provide shoreline resilience. Collaborative community planning efforts have been initiated to modify hardened shorelines to accommodate tidal marsh migration. At a global scale, efforts to temper the pace of climate change are taking place that could address the impacts of climate change as these restoration efforts mature.

Unfortunately, while these initiatives are encouraging, they are not directed specifically at the conservation of tidal wetland plant species diversity per se. That diversity is associated with high tidal marsh, not low marsh. If we are to conserve this diversity, it will be necessary to allow tidal marshes to migrate landward over remaining terrestrial lowlands so that they can form more extensive high marsh and transition zones. Remnant populations of existing marginal species can provide the natural capital for restoration projects. Of course, conservation of these remnant, source populations is critical.

It will take time and opportunity for California's tidal wetlands to adapt and retain their extraordinary diversity. Creating this opportunity is our great challenge. Yet, including the goal of conserving this diversity is the first principle of future success. Just as human agency has created this crisis, human investment, creativity, and action potentially can ameliorate the loss of California's tidal wetlands and provide a bridge for their future survival, including major components of plant species diversity. Organizations like the CNPS that promote conscientious stewardship, restoration, and citizen science are vital to keeping this hope alive.

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DOWN BY THE RIVER: RIPARIAN FORESTS OF CALIFORNIA

Bruce Orr & Amy Merrill

Most of us have fond and vivid memories of riparian forests. Maybe it is a childhood memory of playing on a rope swing hanging from a large valley oak (*Quercus lobata*) or a Fremont cottonwood (*Populus fremontii*) tree overhanging a favorite swimming hole on a Central Valley river, or the cool shade provided by the willows (*Salix* spp.), white alders (*Alnus rhombifolia*), western sycamores (*Platanus racemosa*), bigleaf maples (*Acer macrophyllum*), and coast live oaks (*Quercus agrifolia*) as you hiked along a coastal stream in Southern California on a warm summer day. Or the breeze rustling the leaves of quaking aspen (*Populus tremuloides*), black cottonwood (*P. trichocarpa*), or willows along a stream in the Eastern Sierra as you prepared for an afternoon picnic. Whatever the particular memory, it is likely to include pleasant sensory impressions of cooler air under the canopy provided by broadleaved trees that created dappled patterns of sunlight and shade on the water, stream banks, and riparian forest floor. California supports a wonderful diversity of

riparian forests. Here we briefly explore the diversity, beauty, ecological value, and conservation needs of these critically important ecosystems.

Riparian forests are, by definition, associated with rivers. *Ripa* is Latin for “river bank” after all, and in common usage, riparian is often used to refer to vegetation adjacent to lakes and other water bodies in addition to rivers and streams. Rivers naturally create, maintain, destroy, and recreate riparian forests and, in doing so, maintain river corridors as rich and dynamic places that are continuously responding to conditions upstream and upslope. Riparian forest plants depend upon surface water and subsurface groundwater. Thus, most riparian plant species are considered facultative or obligate phreatophytes: plants that, respectively, sometimes or always depend on water in the channel or in the channel’s shallow alluvial aquifer (see Braudrick et al. this issue).

The growth and survival of riparian forests are tightly linked to the actions of rivers and streams. Forceful winter and early spring flows scour debris and organic material from the banks and floodplains, creating fresh surfaces of bare mineral soil suitable for seed germination in spring. For an individual tree, such

Above: Along this interior lowland river corridor of the Klamath Mountains, species like bigleaf maple (*Acer macrophyllum*) and white alder (*Alnus rhombifolia*) thrive. Pictured here is the Trinity River. Photo by Michael Kauffmann.

as the iconic Fremont cottonwood of Central Valley riparian forests, its future is determined the moment the cotton-light seed makes landfall, via wind or water, typically in early- to mid-spring. If it lands in a viable location, germination will occur in synchrony with receding spring flows. Soil, shade, water access, and river flows are all spatially dependent and critical to the seed's germination, establishment, survival, and ultimately, reproductive success.

The newly-germinated root radical must emerge in moist mineral soil, then follow the saturated soil as stream flows taper in late spring and summer. If deposited too close to the water's edge, subsequent spring and summer flows may kill the seedling by drowning or scour. If deposited too far above the water's edge, death by desiccation awaits. Cohorts of pioneer riparian species, such as cottonwoods and willow, establish on these fluvial geomorphic surfaces when conditions meet the "Goldilocks" criterion of being just right.

Riparian forests abound along reaches where the river slows and meanders across a widened valley floor. Over time, through fits and spates of flood and upheaval, or through slow grinding away at outer bend banks, the river takes down the riparian forests, bringing the trees into the channel. Here the trees become important aquatic habitat, while on the inside of the meander bend the river creates sand and gravel bars with fresh mineral surfaces on which other plants can grow. Riparian corridors are dynamic disturbance-driven landscapes, creating the classic "shifting mosaic" of seral stage and age loosely patterned after the rivers' movement and flood frequency over time.

In addition to a diversity of plants, riparian habitats in California host more than 225 species of birds, mammals, reptiles, and amphibians (RHJV 2004, Olson and Leppig, this issue). Riparian forests provide material that creates diverse habitat structure for aquatic species, and other benefits such as high flow accommodation to reduce downstream flooding, groundwater recharge, water quality improvements, sediment storage, and carbon sequestration.

OVERVIEW OF THE MAJOR RIPARIAN FOREST TYPES OF CALIFORNIA

California wildlife biologists have grouped the state's many riparian vegetation types (see Table 1 and Sawyer et al. 2009) into three broad categories of riparian habitat: valley and foothill riparian, montane riparian, and desert riparian (Meyer and Laudenslayer 1988, RHJV 2004). We focus here on the riparian vegetation and



Montane riparian forests in the Eastern Sierra often exhibit vivid colors in autumn as the dominant trees of quaking aspen (*Populus tremuloides*) or black cottonwood (*P. trichocarpa*) prepare to shed their leaves. Shown here are colorful aspens lining a stream channel in Mono County near Conway Summit. Photo by Bruce Orr.

habitat types dominated by trees (i.e., riparian forests and woodlands – see Table 1).

VALLEY AND FOOTHILL RIPARIAN FORESTS

Large, low gradient rivers of the Central Valley are home to remnant stands of Fremont cottonwood forest, often with various willow tree species including Goodding's black willow (*Salix gooddingii*), Pacific willow (*S. lucida* ssp. *lasianдра*), and red willow (*S. laevigata*), as well as western sycamore (Vaghti and Greco 2007). Stands of valley oak, mixed with white alder, Oregon ash (*Fraxinus latifolia*), Northern California black walnut (*Juglans hindsii*), and box elder (*Acer negundo*) occur on slightly higher terrain, with deeper soils. Curtains formed by lianas of California grape (*Vitis californica*), poison oak (*Toxicodendron diversilobum*), creek clematis (*Clematis linguisticifolia*), and California pipevine (*Aristolochia californica*) extend from the forest floor to the tree limbs above; wild cucumber (*Marah fabaceus*) and California blackberry (*Rubus ursinus*) crawl along the forest floor among patches of shrubby thickets and forbs.

Fremont cottonwood also dominates riparian forests along the inland portion of coastal rivers, such as the Salinas, Santa Clara, Ventura, and Santa Ana. Small stands also scatter across California's desert in palm oases and river bottomlands. Similarly, valley oak may also occur in riparian settings beyond the Central Valley. Sycamore is often a component of mixed

TABLE 1. PRIMARY TREE-DOMINATED RIPARIAN FOREST AND WOODLAND ALLIANCES IN CALIFORNIA AND THEIR REPRESENTATION IN MAJOR RIPARIAN WILDLIFE HABITAT REGIONS.

RECOGNIZED RIPARIAN FOREST AND WOODLAND ALLIANCES ¹	MAJOR RIPARIAN REGIONS ²		
	Valley Foothill	Montane	Desert ³
<i>Acer macrophyllum</i> ⁴ Forest Alliance • Bigleaf Maple forest	X	X	
<i>Acer negundo</i> Forest Alliance • Box-elder forest	X		
<i>Alnus rhombifolia</i> Forest Alliance • White alder groves	X	X	
<i>Alnus rubra</i> ⁴ Forest Alliance • Red alder forest	X		
<i>Betula occidentalis</i> ⁵ Shrubland Alliance • Water birch thickets		X	
<i>Callitropsis sargentii</i> ⁴ Woodland Alliance • Sargent cypress woodland	X		
<i>Calocedrus decurrens</i> ⁴ Forest Alliance • Incense-cedar forest	X	X	
<i>Cephalanthus occidentalis</i> ⁵ Shrubland Alliance • Button willow thickets	X		
<i>Chamaecyparis lawsoniana</i> ⁴ Woodland Alliance • Port Orford-cedar woodland	X	X	
<i>Chilopsis linearis</i> Woodland Alliance • Desert willow woodland			X
<i>Eucalyptus (globulus, camaldulensis)</i> ⁴ Semi-Natural Woodland Stands ⁶ • Eucalyptus groves	X		
<i>Fraxinus latifolia</i> Forest Alliance • Oregon ash groves	X	X	
<i>Juglans californica</i> ⁴ Woodland Alliance • California walnut groves	X		
<i>Juglans hindsii</i> and Hybrids Special and Semi-Natural Woodland Stands ⁶ • Hind's walnut and related stands	X		
<i>Parkinsonia florida</i> - <i>Olneya tesota</i> Woodland Alliance • Blue palo verde - Ironwood Woodland			X
<i>Pinus contorta</i> subsp. <i>murrayana</i> ⁴ Forest Alliance • Lodgepole pine forest		X	
<i>Pinus ponderosa</i> ⁴ Forest Alliance • Ponderosa pine forest	X	X	
<i>Platanus racemosa</i> Woodland Alliance • California sycamore woodlands	X		
<i>Populus fremontii</i> Forest Alliance • Fremont cottonwood forest	X		X
<i>Populus tremuloides</i> ⁴ Forest Alliance • Aspen groves		X	
<i>Populus trichocarpa</i> Forest Alliance • Black cottonwood forest	X	X	
<i>Prosopis glandulosa</i> Woodland Alliance • Mesquite bosque, mesquite thicket			X
<i>Prosopis pubescens</i> Woodland Alliance • Screwbean mesquite bosque			X
<i>Psoralea arguta</i> Woodland Alliance • Smoke tree woodland			X
<i>Quercus lobata</i> ⁴ Woodland Alliance • Valley oak woodland	X	X	
<i>Salix gooddingii</i> Woodland Alliance • Black willow thickets	X		X
<i>Salix laevigata</i> Woodland Alliance • Red willow thickets	X		X
<i>Salix lasiolepis</i> ⁵ Shrubland Alliance • Arroyo willow thickets	X	X	X
<i>Salix lucida</i> Woodland Alliance • Shining willow thickets	X	X	
<i>Schinus (molle, terebinthifolius)</i> – <i>Myoporum laetum</i> Semi-Natural Woodland ⁶ • Pepper tree or Myoporum	X		
<i>Sequoia sempervirens</i> ⁴ Forest Alliance • Redwood forest	X		
<i>Tamarix</i> spp. ⁵ Semi-Natural Shrubland Stands ⁶ • Tamarisk thickets	X		X
<i>Umbellularia californica</i> ⁴ Forest Alliance • California bay forest	X		
<i>Washingtonia filifera</i> Woodland Alliance • California fan palm oasis			X

1. Based on alliances described in the *Manual of California Vegetation, Second Edition* (Sawyer et al. 2009).

2. Based primarily on published and online information for the California Wildlife Habitat Relationships system (especially Meyer and Laudenslayer 1988, CDFG 2005)

3. Includes Desert Riparian, Desert Wash, and Palm Oasis WHR habitat types (Meyer and Laudenslayer 1988, CDFG 2005)

4. This alliance may also occur in non-riparian (upland) environments

5. Treated as a shrubland type by Sawyer et al. (2009), but included as a riparian or wetland type in their “key to forests and woodlands in California.” Under favorable conditions the dominant species in these types can take on a small tree form to create a woodland rather than a shrub thicket.

6. Semi-natural stands refer to alliances dominated by non-native species.



Valley Oak (*Quercus lobata*) Riparian Forest occurs on higher floodplain surfaces in the Central Valley, pictured here along the Cosumnes River. Photo by Bruce Orr.



The Klamath Mountains harbor the only Port Orford-cedar (*Chamaecyparis lawsoniana*) riparian forest alliance in California. Pictured here along Clear Creek in the Siskiyou Wilderness. Photo by Michael Kauffmann.

riparian forests in the Central Valley and Southern California, but it also is found in relatively pure stands forming sycamore woodland, which is one of the rarest riparian forest types in California (Sawyer et al. 2009). It is best developed in alluvial river valleys in the Coast Ranges from Alameda County south to San Luis Obispo and along some streams in the western foothills of the Sierra Nevada.

White alder riparian forests are found along the coastal and inland foothill rivers from San Diego to Del Norte County, occurring inland more often north of Point Reyes. All alders are early seral nitrogen-fixing species that grow quickly; white alders may live to 100 years. White alder cohorts occupy banks and depositional features along foothill and coastal streams where river bends create sunny openings and room for gravel bar deposits or scouring. This species prefers mineral soil and full sun, often forming narrow strips of sentinels along the channel edge. Native poison oak, along with California rose (*Rosa californica*), various species of dogwood (red osier, flowering, brown, and miner's flowering dogwood: *Cornus sericea*, *C. nutallii*, *C. glabrata*, and *C. sessilis*), and torrent sedge (*Carex nudata*) are common co-denizens with this important riparian species. In the Sierra Nevada foothills, white alder often co-occurs with Oregon ash, western sycamore, and Fremont cottonwood, along with shrubby stands of willows and mulefat (*Baccharis salicifolia*). Ponderosa pine (*Pinus ponderosa*) also occurs in some Sierra foothill riparian areas. In the foothill streams of Southern California, white alder often co-occurs with western sycamore, bigleaf maple, and various willows.

Red alder stands hug the northern and central California coastline. In the central and southern portions of the north coast, red alder is quite faithful to the riparian corridor. Farther north however, red alder moves beyond the banks, floodplains, and riparian areas to occupy mesic upland slopes in forest openings. Their small light seeds can survive on wet rotten wood and duff as well as in areas with direct contact with moist mineral soil. Red alder often co-occurs with hardwoods such as black cottonwood and bigleaf maple, and conifers like Douglas-fir (*Pseudotsuga menziesii*) or western red cedar (*Thuja plicata*). Moving away from the river channel, red alder forests typically grade into mixed hardwood-conifer or conifer-dominated vegetation. A particularly awe-inspiring transition occurs in remnant old growth alluvial redwood forests along the South Fork Eel River in Humboldt Redwoods State Park, where the narrow strip of red alder or black cottonwood gives way to ancient coast redwoods (*Sequoia sempervirens*) towering high above the floodplain.

MONTANE RIPARIAN FORESTS

The white alder and mixed riparian forests of the foothills may extend into the montane riparian zone, but as elevation increases, they typically give way to riparian forests dominated by black cottonwood and various willows or thickets of mountain alder (*Alnus incana* subsp. *tenuifolia*) and red osier dogwood. At higher elevations, broadleaved riparian trees are less common and conifers may form the primary tree component of the riparian habitat with an understory



California fan palm (*Washingtonia filifera*) oases can only be found in California's Colorado and Sonoran deserts. Photo by Gordon Leppig.

of shrubs and sedge meadow.

The montane riparian forests along larger streams of the Eastern Sierra and the Modoc Plateau are often dominated by quaking aspen and black cottonwood with thickets of mountain alder, willows, and red osier dogwood. Stream banks often support a lush herbaceous understory laden with summer wildflowers. In some areas, lodgepole (*Pinus contorta* subsp. *murrayana*), Jeffrey pine (*P. jeffreyi*), or narrow-leaved cottonwood (*Populus angustifolia*) are present. Along some of the streams draining into the Owens Valley, ponderosa pine replaces Jeffrey pine at lower elevations as montane riparian forest grades into a high desert riparian woodland.

DESERT RIPARIAN FORESTS AND WOODLANDS

Fremont cottonwood and Goodding's black willow riparian forests also occur in California's desert regions near sources of perennial surface water or shallow groundwater, particularly along alluvial valley bottoms. They are often associated with mesquite bosque dominated by honey or screwbean mesquite (*Prosopis glandulosa* and *P. pubescens*). Similar to the Central Valley and elsewhere, loss of floodplain habitat to agricultural development, and stresses created by water diversions, groundwater pumping, and invasive species, particularly tamarisk (*Tamarix* spp.), have combined to greatly reduce the extent of this once extensive and valuable riparian forest habitat.

California fan palm (*Washingtonia filifera*) oases are a unique type of desert riparian woodland found along the mountain fault systems in the Colorado and Sonoran Desert where groundwater emerges to provide a reliable year-round water supply. The seeps and springs supporting the palms occur in desert washes subject to high flow events that may also promote establishment of Fremont cottonwoods and Goodding's black willows. Desert washes with relatively shallow groundwater but more ephemeral surface flow often support a drier form of riparian woodland known as a desert wash or microphyll woodland that provides valuable wildlife habitat, dominated by species such as palo verde (*Parkinsonia* spp.) and ironwood (*Olneya tesota*).

CONSERVATION CHALLENGES AND SOLUTIONS

In this rapidly changing world, California's riparian areas are threatened on multiple fronts including increasing temperatures and wildfire, reduced and altered river flows, drought, disease, and invasive plant and insect species. Widespread agricultural development in the 19th and 20th centuries reduced the area of native riparian vegetation in the Central Valley to 5–10 percent of the pre-settlement extent (Vaghti and Greco 2007). Flow regulation and levees on nearly all major rivers and streams have created less dynamic rivers, including flow regimes that are often out of sync with native plant phenology. Only a few cohorts of young pioneer tree species line our larger, managed rivers, suggesting limited recruitment and subsequent survival of these foundational riparian tree species, particularly Fremont cottonwood.

In the mountains, streams offer wet, cool refuge in conifer-dominated landscapes. However, even these areas are impacted by changing conditions and human alterations. Although the typical moist and humid conditions of riparian corridors have historically abated wildfires, increased fuel loads, aridification, and in some cases increased extent of flammable invasive species such as giant reed (*Arundo donax*), have converted some riparian corridors to wicks, conducting rather than blocking fire movement across the landscape (Lambert et al. 2010, Merrill et al. 2018).

In spite of continuing threats to riparian ecosystems, multiple success stories shine a light on the path ahead. Widespread recognition of the ecological values of riparian ecosystems in California and the western United States began in the 1970s and 80s (Sands 1977, Johnson et al. *in press*) and a series of confer-

ences over the last 40 years have greatly advanced our understanding of riparian habitats and improved conservation and management of more resilient riparian ecosystems (Ralston and Sarr 2017, Johnson et al *in press*). The most recent conference on the ecology and management of California riparian ecosystems, held at U.C. Davis in October 2017 and attended by more than 400 people, provided examples of new approaches, many cases studies, and promoted a renewed call to action in riparian restoration and conservation (ripariansummit.ucdavis.edu). Despite enormous losses of native riparian habitat in the 19th and 20th centuries and continuing threats in the 21st century, multiple restoration and protection efforts are helping to bring back the critical function and beauty of these ecosystems in areas across the state.

River and riparian conservation and restoration practices have evolved to focus more on maintaining or restoring river processes, incorporating a watershed and landscape-scale perspective, recharging groundwater and maintaining healthy headwaters, promoting river-floodplain connectivity (including setting back levees to give the river more room to function), and emphasizing green bioengineered infrastructure when possible in place of riprap, levees, and concrete channels (Rasmussen and Orr 2017). In the Sierras, efforts to more actively manage montane riparian corridors, formerly treated with hands-off protective approach, are moving forward with recognition that fire suppression has impacted these areas as well as their adjacent uplands (Merrill et al. 2018). While diversions and dams greatly reduced the lateral extent of many riparian corridors in the Central Valley and elsewhere in California, an increasing number of dams are now managed to provide ecological flows, in which dam releases partially mimic the natural flow patterns to better support native riparian and aquatic species and their habitats. In some cases, dams are being removed: the removal of the Klamath River dams (slated for 2021) represents the most significant dam removal and river restoration effort ever attempted in the U.S. and would restore anadromous fish access to potentially hundreds of miles of mainstem river and tributary habitat and include active riparian restoration along approximately 18 miles of river and tributary confluences currently inundated by the four reservoirs.

A number of large rivers now boast large tracts where historical floodplains previously reclaimed for farmland are being restored through levee breaches to promote natural revegetation processes; recruitment on some of these reconnected floodplains is supple-

mented with active replanting of native riparian trees and shrubs. Enhancement and partial rehabilitation of urban streams, including the famously (iconically) cemented Los Angeles River, to provide multiple ecological and societal benefits are also underway. However, there will be no resting on our laurels as threats to our river-riparian ecosystems will continue and likely increase. We hope the successes and lessons learned to date will inspire and inform accelerated actions to restore and protect many more acres of California's beautiful and ecologically critical riparian forests.

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VERNAL POOLS: BIODIVERSITY, BIOGEOGRAPHY, THREATS, AND CONSERVATION

Carol W. Witham, Jennifer Buck-Diaz, & Robert F. Holland

Vernal pools are one of the most fleeting and dynamic environments in California. They occur across the state from the Great Valley to the Sierra Foothills, Modoc Plateau, and the Coast Ranges. While found in many diverse regions of the state, on a localized scale the acreage of vernal pools is scant. Individual pools and small clusters of interconnected pools exist within a matrix of more common vegetation types like grasslands, woodlands, chaparral, and scrub. When compared to nearby natural communities, the ecology and phenology of vernal pools is also vastly different.

Vernal pools form where there is an impermeable layer, or aquitard, just below the soil surface. The impermeable layer can be a variety of substrates including hardpan, claypan, or rock. As rainfall accumulates

on top of the aquitard, a perched water table is created in low spots in the landscape. While many places in the world support similar temporary rain puddles, dramatic, species-rich displays of wildflowers occur only where there are mild wet winters and hot dry summers. California is unique in having a Mediterranean-type climate and an abundance of geomorphic conditions and associated soil types that support the development of a rich flora within vernal pools.

ADAPTATION AND SPECIALIZATION

Vernal pools are seasonal wetlands that fill during winter rain storms and slowly dry as spring progresses. In the summer and early fall, they remain completely dry until rains return. This annual cycle of flood and drought creates extreme—in fact, hostile—conditions for organisms that inhabit vernal pools. These extremes also make vernal pools relatively resistant to encroachment by species that are not adapted to this habitat.

Above: Vernal pools surrounded by oak woodland at Phoenix Park, City of Fair Oaks, Sacramento County. Photo by Julie Evens.

Plants that survive in vernal pools have special adaptations that allow them to endure the annual cycle of flood and drought. One of these adaptations is early germinations after fall rainstorms. Later, when the pool is inundated, some plants have the ability to pipe air to their roots through long, hollow stems or leaves. Others produce floating leaves which absorb enough air for the entire plant. These floating leaves also shade out competition. A number of species, particularly those of deeper vernal pools, will spend weeks or months completely submerged and survive by absorbing dissolved gases directly from the water.

Most vernal pool plants are annuals, living only during the short winter and spring growing season before setting seed and dying. They tend to be of small stature, but with relatively large showy flowers. Diminutive sizes and short lifecycles allow plants to allocate precious energy resources for increased seed production. The showy flowers—with species blooming in mass synchrony—attract a diverse abundance of pollinators. While many types of insects pollinate vernal pool flowers, some native specialist bees (family Andrenidae) have evolved to depend on only one, or a few closely related, species. The bees use the pollen from the flowers to provide food for their developing offspring. The flowers, in turn, depend on bees for pollination. (For more information, visit vernalpools.org/Thorp.)

Vernal pool plants also have an unusual approach to seed dispersal—they don't do it. While most species have no mechanism for dispersal, others have evolved ways to prevent it altogether. Some species plant their seeds into the soil by extending their peduncles into damp mud. Others glue their seeds to the soil surface through sticky excretions on seed coats. Non-dispersal is a beneficial ecological advantage because seeds are retained within these specialized favorable habitats. In this way, seeds are not wasted by dispersal into suboptimal habitats.

Analogous to islands, vernal pools are isolated habitats, thus vernal pool plants have undergone strong selective forces for morphological specialization and speciation. Short-distance pollen foraging by specialist native bees combined with poor seed dispersal limits long-distance gene flow. These combined influences have resulted in a wealth of vernal pool neoendemics—recently evolved clusters of closely related species restricted to vernal pool habitats. The abundance of closely related and similar appearing plants is especially evident in genera like downingia (*Downingia*), goldfields (*Lasthenia*), meadowfoam (*Limnanthes*), mesa

mints (*Pogogyne*), popcornflowers (*Plagiobothrys*), and button celery (*Eryngium*). As you travel between regions of the state, the pools may appear vegetatively similar but species within these genera will often change to ones that are specially adapted to the local conditions.

Parallel evolutionary forces have also resulted in a profusion of aquatic animals endemic to vernal pools. While most of the aquatic organisms are microscopic, numerous larger freshwater crustaceans can be observed swimming and feeding in the pools; most notable are the fairy shrimp (order Anostraca) and the tadpole shrimp (order Notostraca). These crustaceans survive summer drought by producing resting eggs or “cysts.” A cyst is 4,000 undifferentiated cells encased in a hard shell, capable of transforming into a fully developed embryo within hours. The shell promotes embryonic dormancy to survive the heat and desiccation of summer. When rains return, embryos develop and hatch into larvae which quickly begin eating, growing, and eventually reproducing. This rapid development is a critical advantage when your aquatic world lasts for only a few weeks or months.

While some species are naturally localized and rare, many vernal pool taxa were once much more common and are now imperiled because of historic and ongoing human activities that convert vernal pool landscapes to agriculture or development. Thirty-nine species of vernal pool plants and animals are formally listed under the state or federal Endangered Species Acts. Another 78 taxa are tracked by the California Natural Diversity Database and can be considered rare, threatened, or endangered.

RINGS AROUND THE POSIES

Even a casual observer will notice the concentric rings, ribbons, and patches surrounding vernal pools. Circles of pink, yellow, white, and blue blossoms diagram the complex community types that occupy vernal pools. Early ecologists classified pools based on substrates and locations (Holland 1986). Later they were grouped into regions characterized by locally restricted plant species (Keeler-Wolf et al. 1998). Dr. Michael Barbour, along with a team of international scientists, took into account the extensive flora of vernal pools and created a fine-scale classification system based on vegetation (Barbour et al. 2007).

At the Group level in the National Vegetation Hierarchy, vernal pools are defined by 17 diagnostic species that assemble in part, or in totality, within most pools across the state. Barbour found these spe-

VERNAL POOL ENDEMIC BIOTA LISTED UNDER THE STATE
OR FEDERAL ENDANGERED SPECIES ACTS.

<u>Common Name</u>	<u>Scientific Name</u>	<u>Status*</u>
Amphibians		
California tiger salamander	<i>Ambystoma californiense</i>	FT/CT
Crustaceans		
Conservancy fairy shrimp	<i>Branchinecta conservatio</i>	FE
longhorn fairy shrimp	<i>Branchinecta longiantenna</i>	FE
Riverside fairy shrimp	<i>Streptocephalus woottoni</i>	FE
San Diego fairy shrimp	<i>Branchinecta sandiegonensis</i>	FE
vernal pool fairy shrimp	<i>Branchinecta lynchi</i>	FT
vernal pool tadpole shrimp	<i>Lepidurus packardii</i>	FE
Insects		
Delta green ground beetle	<i>Elaphrus viridis</i>	FT
Plants		
Boggs Lake hedge-hyssop	<i>Gratiola heterosepala</i>	CE
Burke's goldfields	<i>Lasthenia burkei</i>	FE/CE
Butte County meadowfoam	<i>Limnanthes floccosa</i> subsp. <i>californica</i>	FE/CE
California Orcutt grass	<i>Orcuttia californica</i>	FE/CE
Calistoga popcornflower	<i>Plagiobothrys strictus</i>	FE/CT
Colusa grass	<i>Neostaphia colusana</i>	FT/CE
Contra Costa goldfields	<i>Lasthenia conjugens</i>	FE
Crampton's tuctoria or Solano grass	<i>Tuctoria mucronata</i>	FE/CE
Cuyamaca Lake downingia	<i>Downingia concolor</i> var. <i>brevior</i>	CE
few-flowered navarretia	<i>Navarretia leucocephala</i> subsp. <i>pauciflora</i>	FE/CT
Greene's tuctoria	<i>Tuctoria greenei</i>	FE/CR
hairy Orcutt grass	<i>Orcuttia pilosa</i>	FE/CE
Hoover's spurge	<i>Euphorbia hooveri</i>	FT
Lake County stonecrop	<i>Sedella leiocarpa</i>	FE/CE
Loch Lomond button-celery	<i>Eryngium constancei</i>	FE/CE
many-flowered navarretia	<i>Navarretia leucocephala</i> subsp. <i>plieantha</i>	FE/CE
Otay Mesa mint	<i>Pogogyne nudiuscula</i>	FE/CE
Parish's meadowfoam	<i>Limnanthes alba</i> ssp. <i>parishii</i>	CE
Point Reyes meadowfoam	<i>Limnanthes douglasii</i> subsp. <i>sulphurea</i>	CE
Sacramento Orcutt grass	<i>Orcuttia viscida</i>	FE/CE
San Diego button-celery	<i>Eryngium aristulatum</i> var. <i>parishii</i>	FE/CE
San Diego mesa mint	<i>Pogogyne abramsii</i>	FE/CE
San Diego thorn-mint	<i>Acanthomintha ilicifolia</i>	FE/CE
San Jacinto Valley crownscale	<i>Atriplex coronata</i> var. <i>notatior</i>	FE
San Joaquin Valley Orcutt grass	<i>Orcuttia inaequalis</i>	FT/CE
Sebastopol meadowfoam	<i>Limnanthes vinculans</i>	FE/CE
slender Orcutt grass	<i>Orcuttia tenuis</i>	FT/CE
Sonoma sunshine	<i>Blennosperma bakeri</i>	FE/CE
spreading navarretia	<i>Navarretia fossalis</i>	FT
succulent owl's-clover	<i>Castilleja campestris</i> var. <i>succulenta</i>	FT/CE
thread-leaved brodiaea	<i>Brodiaea filifolia</i>	FT/CE

*Status: FE = federal endangered; FT = federal threatened; CE = California endangered;
CR = California rare; CT = California threatened.



Vernal pool vegetation showing the typical rings of flowers at Grasslands State Park, Merced County. Photo by Doug Wechsler.

cies represent California vernal pool vegetation across varying aquitard types, soil chemistry, or inundation duration. This class includes pool endemics such as goldfields and mesa mints, as well as more widespread species like American pillwort (*Pilularia*) and water starwort (*Callitriche*). In combination, these species differentiate pools from surrounding upland vegetation and other wetlands—including playas and saline sinks.

The Barbour project also demonstrated that community diversity is high with nearly 50 vernal pool natural community associations nested under 13 alliances. While some pools consisted of just one community, on average they have two to three zones, typically controlled by water depth or other microhabitat changes. Community types repeat from pool to pool and, while some are rare, others are more widespread. The vernal pool plant communities described in the Barbour study have been integrated into the vegetation hierarchy used across California. *The Manual of California Vegetation* (Sawyer et al. 2009) catalogues these types.

Thanks to the work of pioneering vernal pool ecologists, the Barbour Team, and the CNPS Vegetation Program there are now more than 3,000 vernal pool surveys compiled into a publicly available statewide database. While vernal pools of the Great Valley have been extensively surveyed, classification is still needed in other areas of the state such as the Modoc Plateau, Coast Ranges, Southern California, and Baja California, Mexico. Isolated vernal pools also occur in

seemingly unlikely places elsewhere in the state including Fraser Point on Santa Cruz Island, Macdoel in Siskiyou County, and Pioneer Basin in Fresno County. By far the greatest density of vernal pools occurs in the Great Valley, and it is here that they are subject to the greatest threats and continuing loss.

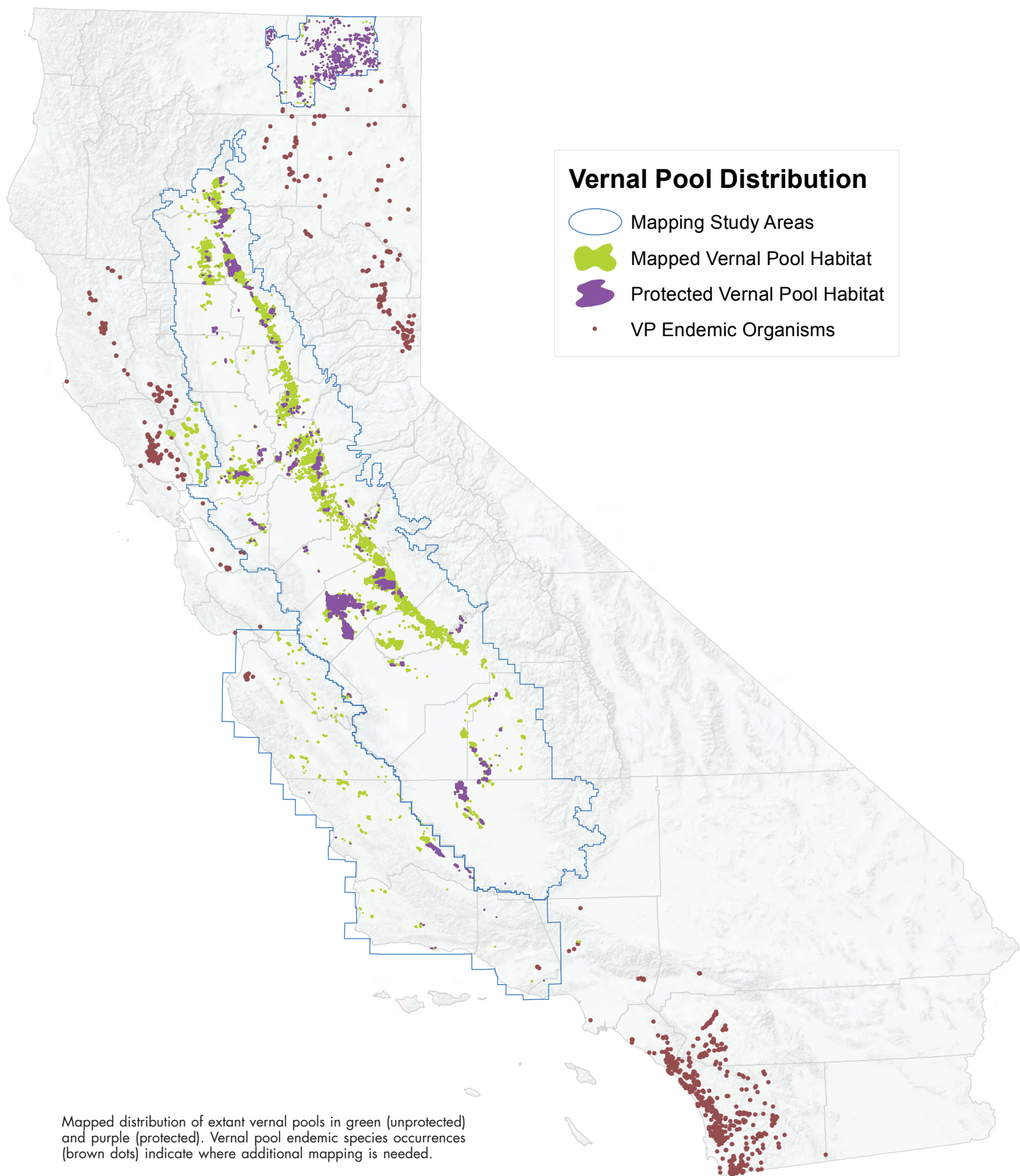
DISTRIBUTION AND (RE-(RE-))MAPPING

The first map of Great Valley vernal pools was published in 1978 by the California Native Plant Society as Special Publication No. 4 (Holland 1978). This map was painstakingly hand drawn from a review of 8,000 individual 30" x 30" black and white aerial photographs. The mapping ultimately

covered a study area of 15.6 million acres and showed that vernal pool habitat occupied over 624,000 acres in, appropriately, a bathtub ring around the valley's perimeter, with a swath along the valley trough.

Fast forward a few decades and a once-primordial Geographic Information Systems (GIS) had matured to the point that agencies and planners began to use it. The US Fish and Wildlife Service was getting ready to prepare a recovery plan for vernal pools and asked Dr. Bob Holland to prepare a new map using this new technology. This second vernal pool map was prepared from interpretation of 35 mm slides (at a scale of about 1 square mile per slide and taken between 1976 and 1995). Identified habitat was hand drawn onto USGS topographic maps which were subsequently digitized into a GIS mapping framework. In 1997, this map was compared with 1996 satellite imagery and updated to show changes in vernal pool habitat since the original slides were taken.

The result was the first widely-circulated digital map of California vernal pools. The second map of the Great Valley vernal pools covered a study area of around 18 million acres. Between the time of the original 35 mm overflights and the 1996 satellite imagery, vernal pool habitat decreased by 37,245 acres (from 1.04 million acres to 1.01 million acres). A subsequent review of this map against 2005 imagery showed an additional 99,475 acres of loss bringing the extant habitat down to 914,326 acres.



Since the first hand drawn maps, GIS has undergone a significant evolution. A third map of the Great Valley vernal pools was undertaken in 2011. It was created from scratch and was based on 2005 high resolution aerial imagery. This map covered a study area of 21.4 million acres and identified 807,820 acres of vernal pool habitat. Once the 2005 baseline was completed, the map was compared with 2012 imagery to determine losses since publication of the Recovery Plan for Vernal Pool Ecosystems (USFWS 2005). This showed another 47,306 acres of loss during the period of 2005-2012 (Witham et al. 2014).

Regardless of the mapping protocol, the results of comparing each map with a subsequent revision of the same map proves a drastic loss of vernal pool habitat throughout the Great Valley. Losses from earliest baseline (1976-1996) to 1997 were 3.6 percent. During 1997-2005, another 13.2 percent were lost. And during 2005-2012, another 8.6 percent had been lost. Dr. Holland once predicted that at these rates of loss all Great Valley vernal pools would be gone by 2086.

INROADS IN CONSERVATION

If you had asked a decade ago, we would have said that the greatest threat to vernal pools was urban expansion, especially in areas like western Placer County or at the proposed new university town in eastern Merced County. A few years ago it became apparent that the most pressing current threat was from agricultural expansion. Vast areas of former grazing lands are now being planted with almonds, pistachios, olives, and grapes. While urban development is regulated by the state and federal government, agricultural conversion has been entirely unregulated. It is now apparent that some form of mitigation should be required when vernal pools are destroyed. Currently, there is no mitigation required for agricultural conversion.

Despite both the observable habitat conversion and conversion documented by various mapping projects, the 2012 re-mapping of the Great Valley had some unexpected surprises. The extant vernal pool landscape map was intersected with a variety of federal and state agency maps of protected areas. While the type and effectiveness of the land protection is variable, some are being managed for conservation resources and others protected from development. In fact, a full 30 percent (~230,000 acres) of the extant vernal pool habitat in the Great Valley is protected. A similar analysis of the mapped areas of the Modoc Plateau shows that 84 percent (~29,000 acres) is protected, mostly

within the Modoc National Forest. In the southern Coast Ranges, 28 percent (~12,000 acres) is protected in one form or another, mostly in the Carrizo Plains area.

There is still a lot to discover and learn about vernal pools in California and Baja California, Mexico. Mapping data exists for less than half of the areas known to support vernal pools. Vegetation associations and alliances still need to be described for many areas. New species of plants and animals continue to be described. Given the amount of habitat already protected, and ongoing efforts to protect more, we and future generations will be able to continue to study and enjoy the magic and mystery of vernal pools.

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MOUNTAIN MEADOWS: EMERALD OASES OF THE SIERRA NEVADA

Amy Merrill & Nicole Jurjavic

In summer 2015, we visited Osa Meadow on the Kern River Plateau. Driving up the winding road from Kernville to Black Rock Station, we were struck by the bold, stark beauty of the southern Sierra. Peering down a cliff on one side of the road and up at a wall of rock leaning over us on the other side, our eyes sought refuge along the road ahead, where we saw forests and boulders carpeting the extremely steep slopes. At a bend in the road, we peered up a side valley and saw a small patch of green and sunlight: a mountain garden thriving in the raw and rocky landscape. This meadow view reminded us that we were following many people who came before us to harvest from, and tend to, the verdant meadows of the Sierra Nevada mountains.

These people include Native American tribes that occupied the mountains for thousands of years, the 19th and 20th century shepherders, cowboys, and gold prospectors, as well as the 20th and 21st century

Forest Service and Park Service public servants and the California Conservation Corps. Previous generations went to mountain meadows for basket weaving materials, for hunting, and to pasture flocks of sheep and cattle. Cultures managed mountain meadows in various ways over time, using light ground fires, culling and cutting specific plants, installing check dams, grazing sheep and cattle, and suppressing wildfire. Today, we believe our restoration techniques and modern science will guide actions and on-going management to bring Osa Meadow to greater biological diversity.

In the 20th and 21st centuries, Osa Meadow experienced large conflagrations and floods, with the most recent disturbances occurring in summer 2002. In July and August of that summer, the McNally fire burned over 60,700 hectares of Sequoia National Forest, including the watershed surrounding Osa Meadow. That November, the intense burn was followed by a 50 centimeter-burst of rain over 48 hours that drove tons of soil out of the meadow through a newly blown out channel. Because of this and other past events, the

Above: Bonita Meadow near Osa Meadow in Sequoia National Forest. Photo by Amy Merrill.

incised channel has been draining the rooting zone in Osa Meadow for the past 15 years, pulling the wet carpet out from under water-loving sedge and forb species and clearing the way for more summer-drought tolerant plants.

We pulled up to the site after a 10-kilometer dusty drive down a Forest Service road. The cool shade of the fir and pine forest opened to a wide, sunny, and green meadow. Osa Meadow lies within a 6,706 square kilometer subalpine watershed on a 3,000 meter high granite plateau that experiences long periods of deep snow cover punctuated by brief, frenetic growing seasons. Looking across the meadow from the forest edge, we saw a barren rocky hillslope that reached down from the opposite side of the opening; bare granite and gravel meet Nebraska sedge (*Carex nebrascensis*) and spikerush (*Eleocharis* spp.) to delineate a clear boundary between wet and dry. As we tromped across the meadow, we saw many bare soil patches among clusters of Kentucky bluegrass (*Poa pratensis* subsp. *pratensis*), Parish's yampah (*Perideridia parishii* subsp. *latifolia*), and alpine aster (*Oreostemma alpigenum* var. *andersonii*). The channel, with dry banks reaching knee-to-thigh high as we walked along it, was lined with a mix of wet and dry species: Nebraska sedge, Kentucky bluegrass, bentgrass (*Agrostis* spp.) and patches of Lemmon's willow (*Salix lemmonii*). Farther down, water appeared in the channel and water-loving sedges and forbs, including primrose monkeyflower (*Erythranthe primuloides* var. *linearifolius*), bistort (*Bistorta bistortoides*), spikerush, arrowleaf ragwort (*Senecio triangularis*), Nebraska sedge and long-bracted sedge (*Carex athrostachya*) extended from the banks into the belly of the meadow, where small remnant ox bows harbored patches of high productivity. We were there with representatives of CalTrout, Sequoia Forest Keeper, and Sequoia National Forest, to discuss plans to restore Osa Meadow by raising the groundwater level, and then to track the response to restoration by monitoring the hydrology, soil, and plant communities.

Meadows like Osa, each with their own setting, shape, size, and secret treasures, lie scattered across the Sierra Nevada, clustered along tracks of alpine glaciers, lining lakes and adorning stream valleys, and occupying other local topographic minima created by any number of geologic circumstances. The relatively small extent of these meadows, together adding up to just one percent of the entire Sierra Nevada range, belies the ecological importance of these green oases for local denizens.



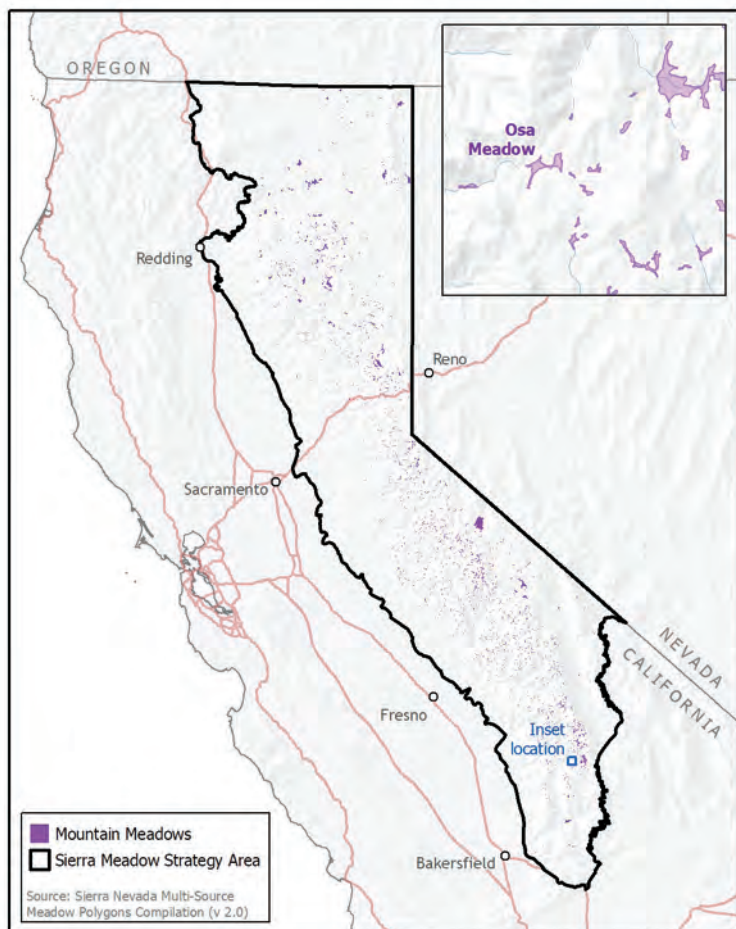
Incised channel at Osa Meadow, August 2015. Photo by Amy Merrill.



Meadow in Eldorado National Forest with a non-incised channel, showing full spring floral display. Photo by Ian Pryor.



Meadow in Eldorado National Forest. Photo by Ian Pryor.



Meadow systems of the Sierra Nevada, Southern Cascades, and Modoc Plateau. Over 18,600 meadows are mapped in the greater Sierra Nevada, occupying over 111,600 hectares. Inset of Osa and surrounding meadows.

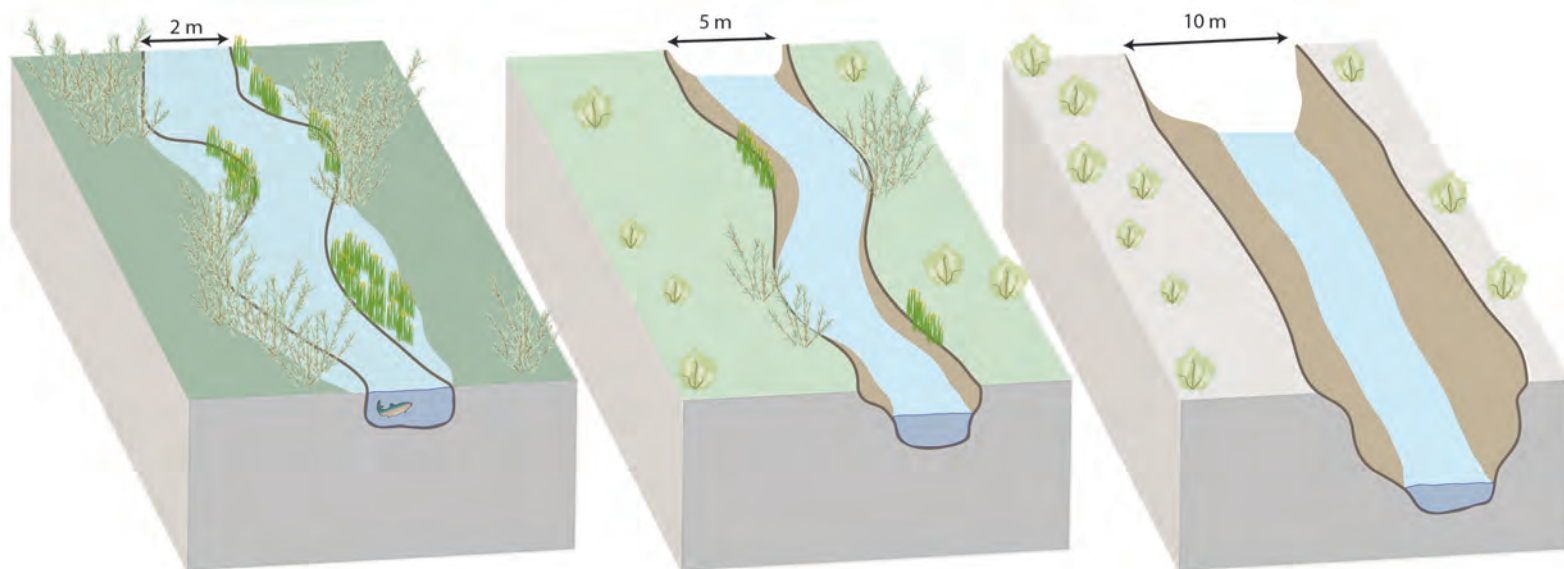
The Sierra Nevada mountain range includes about two-thirds of the bird and mammal species and about half the reptiles and amphibian species native to California. Mountain meadows are considered the single most important summer habitat in the Sierra for birds and are also important habitat for native trout and amphibians (Erman 1996, Siegel and DeSante 1999). Fens, a wet, peat-forming type of meadow, support five federally listed animal species including yellow-legged frog, Cascades frog, Yosemite toad, Owens tui chub, and two state threatened birds: greater sandhill crane and willow flycatcher (Sikes et al. 2012).

These wide ranging environments, with the common denominator of abundant summer sun and early season water, are home to over 1,400 native vascular plant species, including 170 special status species. These species represent over 110 genera and 50 families respectively, as tallied from CalFlora and CNDDDB databases (Calflora 2018; CDFW 2017). The families most abundantly represented with special status species include Cyperaceae, Asteraceae, Ophioglossaceae, and Liliaceae with 23, 12, 11, and 10 listed species respectively. In the CalFlora database, over 500 native vascular non-tree species are reported to occur in meadows but not in the surrounding uplands. These “meadow only” species represent a third of the total meadow-occurring species. On a per hectare basis, meadows support 38 times more native plant species than their surrounding uplands. These numbers, summarized in Table 1, are based upon queries of the CalFlora database in areas above 610 meters, mapped as alpine fell-fields, freshwater wetlands, or wetland-riparian habitats, and extending across the greater Sierra Nevada that includes the Warren Mountains, Modoc Plateau, and Klamath Mountains (CalFlora 2018). For the surrounding forests and uplands, we used the same filters to map the other habitat types.

Besides being biodiversity hotspots, meadows also serve as small reservoirs, recharging groundwater and releasing surface water in the dry season to support downstream fisheries and other aquatic life. As natural alluvial systems, meadows capture and hold surges of sediment from above and mete it out slowly downslope, thereby moderating impacts on downstream habitat. As water seeps through rich meadow soils, decomposition of the year’s lush growth is slowed by the damping effect of high groundwater and low oxygen, so that some meadows become local carbon reservoirs, with the carbon tucked away from forest fire’s releasing effect.

Table 1: Number of non-tree vascular species reported in Sierra uplands compared to those reported for Sierra meadows, and those found in meadows only and not in surrounding uplands (CalFlora 2018).

Environment	Area (hectares)	Native taxa	Native taxa per 3,000 hectares
Forest and Uplands	10,305,213	3,153	1
Meadows	111,646	1,429	38
Meadows only	111,646	509	14



Positive feedbacks as seen in meadow systems. LEFT to RIGHT: A healthy sinuous channel floods frequently with spring runoff, but impacts such as cattle or sheep crowding along channel banks or an undersized culvert can weaken channel banks and focus surface water energy on the channel, resulting in channel widening and incision. This further increases the focus of flows inside the channel, initiating the positive feedback that leads to greatly incised channels surrounded by xeric rather than wet or moist vegetation. Graphic by Karley Rodriguez and Amy Merrill

DEFINITION AND STATUS

While the specifics vary, roughly half of the Sierra Nevada meadows are experiencing challenges like those faced by Osa Meadow, and only a small subset are receiving the attention needed to reverse or redirect degradation. Within the greater Sierra Nevada, the most recent mapping effort reveals 18,600 meadows comprising 111,646 hectares, dusted across an otherwise water limited landscape (UC Davis et al. 2017). The term “meadow” is broad, but here it specifies areas with fine-textured surface soils, dominated by herbaceous vegetation (woody species such as willows and mountain alders are common, but not dominant), with subsurface water within the upper meter of the rooting zone for at least several weeks of the growing season (Weixelman et al. 2011). These conditions can occur mid-slope where a geologic contact creates springs and local wet spots, on alluvial fans where water seeps out from upslope, in rounded glacial valleys filled with variably textured layers of sediment that may include aquicludes, and in wide river valleys swept clean by the river’s millennial (or centennial) cross-valley swing.

This hydro-geomorphic classification encompasses a great diversity of meadow types, including meadows with peat soils such as fens, meadows with standing or slowly moving water and emergent sedges and tules, meadows that line lakes, meadows where the water drops slowly over the summer, and meadows where

the soils become dry as a bone by mid-July. Several studies document the close linkage between meadow hydrologic regime and plant species composition (Hammersmark 2008, Lowry et al. 2011). Water source matters for temporal patterns, response, and vulnerability. Surface snowmelt varies by water year. Stream surface flow depends upon channel form and connectivity to the meadow floodplain as well as upstream sources. Localized depressional meadows can rely on surface water input or precipitation. And meadows receiving water from springs might have delayed responses to variation in water year. However, all these types are vulnerable to vicissitudes of climate change (Veirs et al. 2013).

MEADOW DEGRADATION AND RESTORATION

Euro-American activities in mountain meadows began in the mid-19th century with domestic sheep grazing and then accelerated drastically in the 1860’s. With the gold rush, came intensified sheep and cattle grazing, and meadow channels were moved to the side and straightened to make way for wagon tracks and rail roads. Banks were eroded and head cuts initiated from intense cattle and sheep livestock use. Effects of 20th and 21st century human activities are now added to impacts from earlier times and include waves of logging and associated erosion. Additionally, fire suppression, and a subsequent increase in the frequency



Meadows are home to many uncommon and beautiful native plants. LEFT to RIGHT: Meadow paintbrush (*Castilleja lemmonii*). Photo by Rob Thoms. Northern adder's-tongue (*Ophioglossum pusillum*). Photo by Megan Keever. Mountain meadow beardtongue (*Penstemon rydbergii* var. *oreocharis*). Photo by Rob Thoms. Ranger's buttons (*Angelica capitellata*). Photo by Rob Thoms.

of large wildfires associated with drought, disease, and climate change, also stress mountain meadows.

Positive feedbacks drive impacted meadows through a spiral of change toward drier and less productive systems. For example, as sheep, cattle or even mountain bikes direct spring runoff along a trail or channel bottom, the focused force of water increases the amount of sediment carried off, lowering the channel base level. Bankside plant species composition responds to the greater vertical distance to water, shifting from wet sedge and rush dominated communities to drier site species assemblages composed of annual grasses and sagebrush. These drier plants have less binding root structures, resulting in bank instability and increased channel migration rates. As channel banks lose integrity, the incised channel widens, increasing channel capacity and reducing overbank flows. With peak yearly flows thus captured inside the channel, the power of snowmelt flows and summer showers are focused on the channel rather than distributed across the meadow plain, resulting in more widening and incision that can lead to channels 2 m to 10 m deep. Once in this positive feedback loop, the meadow will only recover to a wetter state with considerable outside effort; suspending grazing or replacing an undersized culvert will not necessarily recover the former form and function of the meadow and channel.

Restoration of hydrologically degraded meadows is often done through some direct action in the channel itself. These actions include: creating a series of check dams; expanding inset floodplains and setting back and stabilizing eroding banks; creating small ponds

from in-situ borrow pits interspersed with dams made with the borrow material (dubbed 'pond and plug'); and enticing local beaver populations to expand into a meadow by building beaver dam analogues (Stillwater Sciences 2012, Pollock et al. 2014). However, the long-term effects and benefits associated with these methods are not well understood or documented.

Conifer encroachment into meadows (mostly lodgepole pine [*Pinus contorta* subsp. *murrayana*] at mid- and lower elevations) has been attributed to several non-exclusive causes including climate, cessation of grazing and fire suppression (for example, see Millar et al. 2004). Water availability and fire regime, both strongly responsive to effects of climate change, are likely to be the most important factors controlling current and future conifer encroachment (Lubetkin et al. 2017). The Forest Service and others are piloting and monitoring conifer reduction and fuels management actions in meadows to better understand how to address conifer encroachment.

THE SIERRA MEADOWS STRATEGY

What can be done to protect, restore, and/or create greater ecological benefits from degraded meadows? What meadows do we prioritize for action? How much will it cost? How do we track and hone our success?

We are not the first to ask these questions but perhaps better poised than our predecessors to answer them, and likely more desperate, given the scale and intensity of threats. Spun out of several places over the past two decades, representatives from agencies,

non-profits, universities, and private practitioners are now joining forces as the Sierra Meadows Partnership to share knowledge, ideas, and resources to improve meadow condition in the greater Sierra Nevada. The Sierra Meadows Strategy lays out a vision for restoring 12,140 hectares—roughly one-third—of degraded meadows in the greater Sierra Nevada over the next 15 years (Drew et al. 2016) by increasing restoration and protection, enhancing funding capacity and coordination, and expanding partnerships. Efforts are underway to achieve these goals with an open group of interested parties. We are at the beginning of this process but already have a knowledgeable and experienced group of ‘meadowphiles’ working toward these common goals. There is much more to be done to restore and maintain mountain meadows for the critical benefits they provide our native plants and wildlife, for the clean cool water they store and release, and to ensure that healthy meadows can be enjoyed by current and future generations.

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PALEOBOTANY OF A COASTAL CALIFORNIAN WETLANDSCAPE

Chelsea Teale & Eileen Hemphill-Haley

Paleoecology is a multidisciplinary field that reconstructs past environments using proxy records, which are non-instrumental sources of information on variables like flora and fauna. Paleobotanists have been influential in developing the paleoecology “toolkit,” which includes identifying vegetation from remains that might be as large as entire tree branches or as small as seed hull fragments. This is important because knowing the habitat requirements of identified plant taxa leads to an understanding of past environments.

As a field, paleobotany tends to refer to deep geologic time; but Quaternary paleobotany, which is the

field most pertinent to paleoecologists, focuses on the past two million years of Earth history. In North America, an especially well-studied time period within the Quaternary is the past few tens of thousands of years because sites and fossils are most thoroughly preserved. In this relatively recent period, “fossil” does not always refer to mineralized, rock-like remains because plants and plant fragments can be soft and even retain their color. Many such specimens that still contain organic material are more correctly called “subfossils,” which are useful in radiocarbon dating (a process used to estimate ages as old as 50,000 years). The contribution of Quaternary paleobotany to paleoecology, therefore, not only includes reconstructing past plant communities by identifying fossil plant taxa but also revealing the ages of those communities.

Large plant fragments, like seeds and leaves, are called macrofossils; those that require high magnification, like pollen, are called microfossils. Each type

Above: The level of detail on maps of Pillar Point Marsh has increased over time. Clockwise from top left: earliest map available for the marsh area (1837), earliest navigational map (1861), earliest topographic map (1896), recent topographic map (2017), recent navigational map (2003), and Google Earth (2018).



Location of Pillar Point Marsh on the north side of Half Moon Bay; the core site was near to the southernmost pond.

relays important information to paleobotanists, and hence to paleoecologists. Macrofossils more accurately reflect environments of the immediate vicinity because they typically accumulate in place, while microfossils may reflect a wider area due to their propensity to be transported by wind, water, or other mechanisms. Wetlands and open water bodies like lakes and ponds are good sources of both fossil types because saturation protects against decomposition (rotting). Plant matter is thus preserved in aquatic basins in the order in which it settles—older material deposited first and the youngest on top—which creates a natural archive of past vegetation.

HISTORICAL ECOLOGY

A subfield of paleoecology, called historical ecology, has emerged in recent decades. This discipline focuses on the recent past to determine what environments were like just prior to human impact. In North America, most historical ecology focuses on the time since European colonization with a goal of identifying



Looking south from the emergent freshwater wetland, dominated by tules, to the tidal estuarine wetland with salt-tolerant species. Pillar Point is to the right. Photo by Chelsea Teale.

the pre-disturbance landscape as a baseline for restoration (Swetnam et al. 1999). In fact, the San Francisco Estuary Institute (SFEI) has made California a leader in historical ecology research. SFEI's goal is to help conservationists restore and protect native landscapes in areas most threatened by development, such as the Bay Area, Sacramento Delta, and Southern California (www.sfei.org). Under the Resilient Landscapes Program, SFEI has produced publicly available reports that enable a greater understanding of the inherent potential in those landscapes; the methods and materials used by SFEI can be applied in many other locations.

In California and elsewhere in North America, historical ecologists must consider the impacts Native Americans had on their environments before European contact, such as hunting, gathering, agriculture, burning, and more. This evidence is sometimes obvious and other times blended with natural processes. A paleobotanical study of Pillar Point Marsh, the largest wetland on Half Moon Bay, provides an example of the kind of historical ecology study done by SFEI in an area long inhabited by Native Americans who actively managed the landscape.

PILLAR POINT MARSH

The National Wetland Inventory classifies Pillar Point Marsh as two wetland types: a 6.5-acre tidal estuarine wetland at low elevation separated from Pillar Point Harbor by a beach berm, and 29 acres of emergent freshwater wetland inland and slightly uphill. A large ephemeral pond—the remains of a coastal lagoon—is drained by a former slough channel through the berm, which historically breached more frequently and regularly during winter storms before a breakwater was built in the harbor in the 1960s. In the dry summer months, this channel may not have sufficient flow to reach the harbor, but enough salt water enters at other

times of year to make the marsh water brackish. Two smaller ponds within the tidal estuarine wetland are not connected to the channel and have different salinities at different times of year depending on contributions from fresh water and salt water sources. Tule (*Schoenoplectus acutus*) and cattail (*Typha* sp.) characterize much of the freshwater wetland inland of the large pond, beyond which is a thicket of willows (*Salix* sp.). Pickleweed (*Salicornia* sp.), jaumea (*Jaumea carnosa*), and alkali heath (*Frankenia salina*) in the estuarine wetland indicate high salinity in the lower basin surrounding the two smaller ponds. Groundwater extraction, and diversion of surface water away from the marsh, may have changed the amount and salinity of water within both types of marshes over the past half-century.

HISTORICAL RECORDS

Questions abound when historical ecologists study a place like Pillar Point Marsh. Has the marsh always looked and functioned this way? If not, how has it changed? Did the local Ohlone tribal people interact with this marsh in any way?

To answer these questions, many types of historical documents can be read to see if there are first-hand descriptions of the area, but not every aspect of a landscape is recorded by every source because the importance of different types of natural resources changes over time. For example, in the northeastern United States and Canada, wetlands are often described by early European settlers because they were important sources of hay and pasture. In California, however, there were sufficient open prairies to satisfy forage needs. It is therefore not surprising that the earliest available map of the Pillar Point area, an 1837 map of the Rando Corral de la Tierra land grant, does not include any details about the marsh.

Historical maps, travel narratives, journals and diaries, and other written sources can also be examined for information. Maps can show if there were documented changes in size and shape of water bodies and channels, or if there were changes in symbols for vegetation type (for example, from shapes signifying grass to others signifying trees). Nautical charts and topographic maps suggest there has been little change in Pillar Point Marsh over the past 150 years.

The Portolá Expedition, the first Spanish overland exploration of California from 1769-1770, followed the coast from San Diego to the San Francisco peninsula and routed around Half Moon Bay. Records survived from three of its members, with the diary of

Father Juan Crespí being the most detailed in the documentation of landscape, vegetation, and activities of indigenous people. Crespí did not note the marsh but did remark upon Pillar Point itself, which he named Punta de Ángel Custodio (Guardian Angels Point). Native Ohlone people lived around Half Moon Bay and Crespí remarked on their villages, diets, clothing, and land-management techniques that included fire (Brown 2001).

“...we set out... from this stream of Saint Ives [probably Purisima Creek near Lobitos], over level land of rolling tablelands of very good soil close to the shore; all the grass had been burnt off... (October 28, 1769)

“Close to the shore, there ran on some tablelands and rolling knolls with very good soil and very good grass, though the latter all burnt, since the heathens burn it all off in order for a better yield of the grass seeds that they eat. (October 30, 1769)

In coastal California, fire induced by lightning is rare but anthropogenic burning has been common for thousands of years (Lightfoot and Cuthrell 2015). It was so common that officials overseeing the missions-presidios-pueblos settlement system were critical of the practice because they believed it threatened the food source of imported cattle. Governor Arrillaga went so far as to forbid burning in May 1793 because of the damage fire was causing to lands the Spanish relied on as pasture (Clar 1959).

Crespí did not describe the prairie flora in his journal but described the upland as pastures (*pastos*) and the knolls as bald (*del todo pelonas*). He did, however, mention eating seeds in the form of cakes which could have been red maids (*Calandrinia menziesii*) or chia (*Salvia columbariae*), two species that would have fit in well with the native forb-dominated California prairie (Anderson et al. 2012; Holstein 2011). He repeatedly emphasized the lack of trees but occasionally noted willows, oaks, hazels, brambles, and roses (Brown 2001). Pollen from these species is present in similarly aged wetland sediments nearby. At a site approximately 60 miles to the north, for example, Quaternary paleobotanists identified redwood (*Sequoia sempervirens*), Douglas-fir (*Pseudotsuga menziesii*), oak (*Quercus*), alder (*Alnus*), tanoak (*Notholithocarpus densiflorus*), and hazel (*Corylus*) with an understory of asters (Asteraceae) and members of the rose family (Rosaceae) (Anderson et al. 2013).

Following the initial Spanish exploration, the area

around Pillar Point became ranchland owned by the Catholic Church and then by a private individual who received the Rancho Corral de la Tierra land grant by the Mexican government. The area came under American control in 1846, and in response to the demand for foodstuffs during the Gold Rush it was used as cattle pasture and vegetable farms. In all of this history, nothing is known of Pillar Point Marsh itself, compelling the historical ecologist to use proxy records

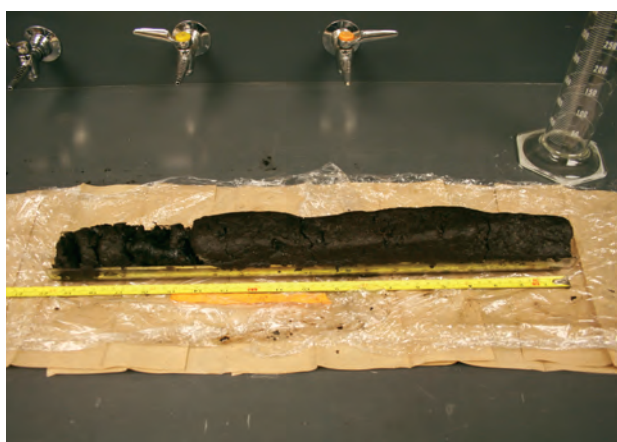
PROXY RECORDS

In 2011, a gouge corer (a specially designed hollow metal tube with a long handle) was inserted into the tidal estuarine portion of Pillar Point Marsh to retrieve a core that extended from 50 to 100 cm below the surface. Diatoms—a type of single-celled algae that secrete microscopic shells of silica and can be used to estimate water salinity—are found at all levels in the core. A visibly sharp contact in the core between coarse peat and an overlying silty loam coincides with a transition from a shell assemblage reflecting diatom species living in a brackish/freshwater marsh to one more characteristic of salt-tolerant species that live in tidal flats or coastal lagoons (Koehler et al. 2005). Paleoseismologists (scientists who study past earthquakes) theorize that the cause of this environmental change was subsidence due to an earthquake, converting an environment that had been above the reach of tides to one that was regularly flooded by seawater. Based on historical records and a limited number of radiocarbon dates, Schwartz et al. (2014) proposed that the earthquake occurred between 1700 and 1776 AD. Interestingly, Crespí described Pillar Point as forming

a cove (*enzénada*; Brown 2001). Although his description is not definitive, it is possible that Crespí was recording the presence of the post-earthquake lagoon. If so, this suggests that the earthquake occurred prior to 1769. Radiocarbon ages for seeds recovered from the peat layer elsewhere in the marsh extend to 1450 AD (Koehler et al. 2005). Based on these dates and paleoclimatological studies of past droughts and wet conditions, this peat probably accumulated during a period of frequent El Niño events and high precipitation in central coastal California (Heusser et al. 2015).

But what were the characteristics of the wetland before it became regularly inundated by seawater? Plant macrofossils are ideal for determining this kind of localized vegetation, so the peat core was cut into 1 cm sections and each section was washed through a screen using tap water to remove silt and clay for better visibility. The leftover material was examined under a low-power microscope. Macrofossils were identified that are indicative of an emergent freshwater marsh, including sedges (Cyperaceae), cattail (*Typha* sp.), rushes (*Juncus* sp.), and knotweeds/smartweeds (Polygonaceae). Floating freshwater taxa like water fern (*Azolla* sp.), water lilies (*Nymphaea* sp.), and marsh pennywort (*Hydrocotyle* sp.) were also common. Seeds of dodder/goldenthrum (*Cuscuta* sp.), indicate that this plant parasite was present; in California tidal marshes, it often targets *Salicornia* and other salt-tolerant species, suggesting that saltwater was present at times. *Amaranthus* (Amaranthaceae) grow on dry soils and were probably present on the surrounding upland.

Water fleas (cladocerans) produce resting eggs called ephippia when conditions are not optimal, such as poor water quality. Sand was common, perhaps result-



The 50 cm peat core ready for subsampling. The oldest layers are to the left and the newest to the right, above which the sediment changes from organic to mineral, indicating a shift from wetland to lagoon. Photo by Chelsea Teale.



A 1 cm thick subsample showing the dark brown, highly organic peat. Photo by Chelsea Teale.



A Humboldt State University student sieving a subsample under running water. This screen has spaces of $125\mu\text{m}$ to prevent very small seeds from passing through. Photo by Chelsea Teale.

ing from beach berm erosion, and charcoal was also found. This charcoal may indicate burning of the marsh itself because such large pieces usually don't travel far from their source. Fire was used by Native Americans in tule wetlands to clear dead stems and stimulate new growth, which also increases the available plant protein. Rhizomes, young shoots, and unripe fruit heads of the tule plant are edible, the achenes can be ground into a kind of flour, and its pollen used as an ingredient in some foods. The plant was also used to make houses, boats, netting, baskets, clothing, footwear, and in medicines (Stevens 2004; Tilley 2012).

Burning dead tule would increase the amount of open water for *Azolla* to thrive and temporarily decrease water quality, thus inducing cladocerans to produce ephippia until water conditions improved. Clearing dead tule would increase the amount of open water for *Azolla* to thrive, while temporarily decreasing water quality that harms cladocerans whose resting eggs wait to hatch until conditions return to normal.

CONCLUSION

Pillar Point Marsh was undoubtedly a historically important site to the Ohlone if it was filled with tule, and plant macrofossils and charcoal suggests the marsh was repeatedly burned. This study is a small scale example of how Quaternary paleobotany can be used by historical ecologists to reconstruct a long-gone wetlandscape—one that until now was not imagined as an important resource in this part of a pre-settlement California.

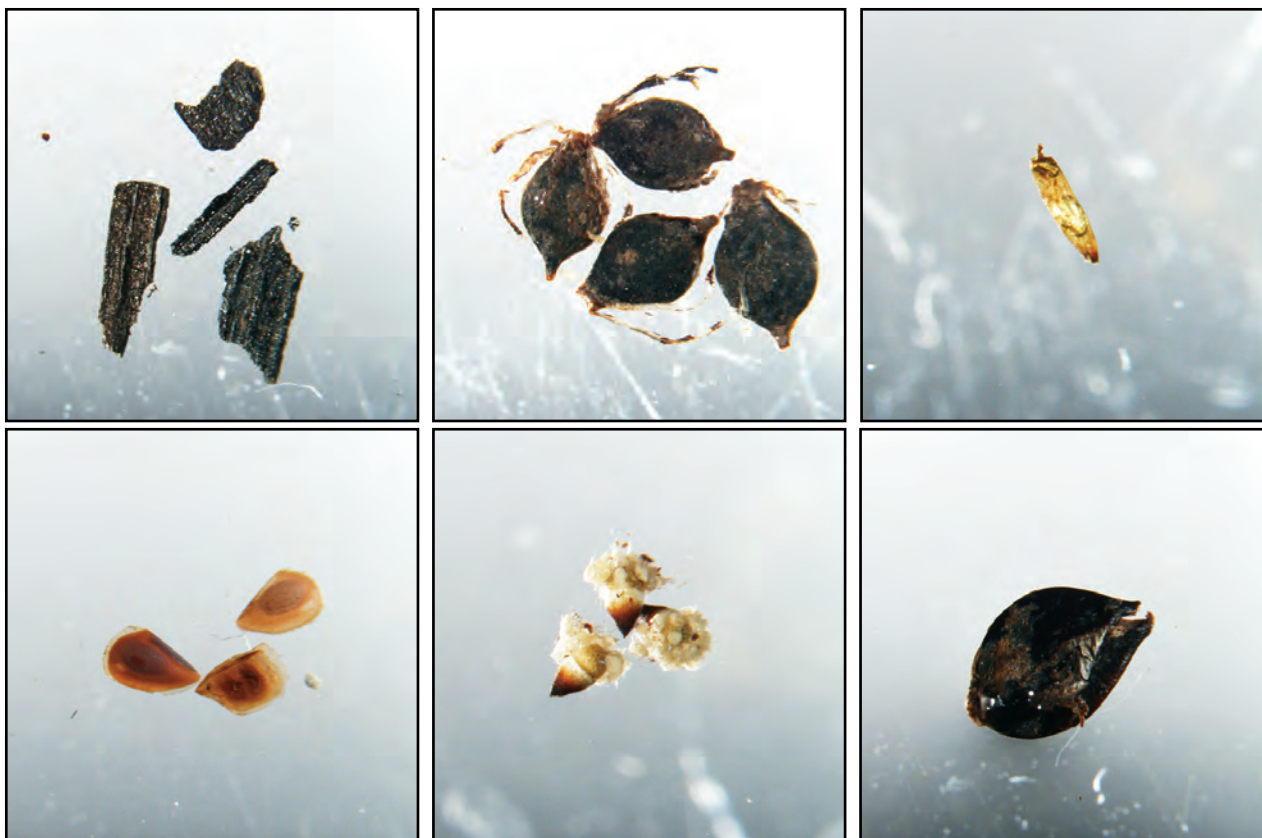
The historical ecologist might now ask if it is desirable to restore the marsh to its pre-settlement form. The goals of restoration vary considerably but often relate to reestablishing natural processes or recreating aesthetically pleasing scenery. In the case of Pillar Point Marsh, there might be a benefit to restoring the tule marsh for the benefit of waterfowl, as is the case at Tule Lake National Wildlife Refuge, where Ducks Unlimited is partnering with several public agencies. One might also argue that towering, dark-green stems of tule and cattail would provide a contrast to the palette of beige and gold that characterize the area today. However, because changes in the marsh were the result of a natural phenomenon (earthquake), Pillar Point Marsh is not a typical candidate for restoration.

Furthermore, is restoration even possible? The answer is probably not, for two reasons. Firstly, urban development and construction of the breakwater have altered the quantity and salinity of water entering and leaving the marsh. Secondly, because the 19th century earthquake caused the marsh surface to sink, it may take a long time for the current peat layer to build up to reach a level that would allow roots to escape salty water. Yet here is another benefit of historical ecology: today. The tidal estuarine portion ("salt marsh") is the highlight of public education efforts at Pillar Point Marsh, but knowing past conditions can prepare us to accept future changes if that wetland type is gradually replaced with freshwater emergent marsh.

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Examples of macrofossils, clockwise from top left: Charcoal, tule (*Schoenoplectus*) achenes, cattail (*Typha*) seed, *Cladoceran* ephippia, water fern (*Azolla* megasporocarps), and Polygonaceae seed. Please note that these images are not at the same scale, but that none of the macrofossils are larger than 5 mm in any dimension.

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GROUNDWATER DEPENDENT ECOSYSTEMS

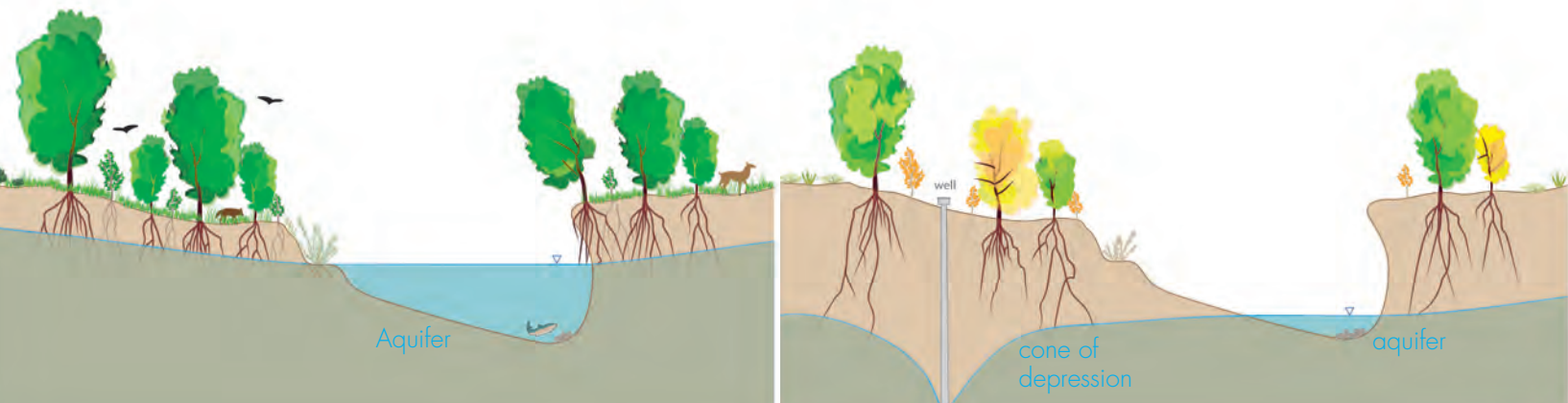
Christian A. Braudrick, Amy G. Merrill, & Bruce K. Orr

Groundwater depletion is widespread throughout California and the western U.S., resulting in significant impacts to water availability and quality for cities and farms. Groundwater pumping can also have serious impacts on the health and survival of riparian and wetland ecosystems (below). To address long-term decreases in groundwater levels in California and impacts associated with that decline, California passed the Sustainable Groundwater Management Act (SGMA) in 2014. The goal of SGMA is to ensure that groundwater use is sustainable and does not have deleterious effects to the beneficial uses of groundwater (see definitions at end). Local stakeholders must form a Groundwater Sustainability Agency (GSA) to develop a Groundwater Sustainability Plan (GSP) by 2020 or 2022, depending on the degree of groundwater overdraft. More than one GSA can be formed in each basin. These plans are required to prevent groundwater conditions from causing any further harm to beneficial uses after 2015 and to work towards making groundwater conditions sustainable within 20 years of plan's submittal. To ensure that sustainability plans are not having adverse effects on beneficial groundwater uses, groundwater and its beneficial uses must be monitored and reported to the Department

of Water Resources every five years after submittal of the plan.

To comply with SGMA, GSAs must ensure that their GSPs consider the impacts of groundwater conditions on groundwater dependent ecosystems (GDEs). The California Department of Water Resources defines GDEs as ecological communities or species that depend on groundwater emerging from aquifers or on groundwater occurring near the ground surface. GDEs occur in a variety of different environments ranging from seeps and springs, to groundwater-dependent wetlands, to aquatic and riparian ecosystems associated with rivers that partially or entirely rely on groundwater.

Although the regulatory requirements for sustainable groundwater management are new in California, there has been extensive research on integrating groundwater management and GDEs that can be used to develop tools to assist GSAs in mapping and assessing the impacts of groundwater management on GDEs in California. Based on this research, The Nature Conservancy has developed a guidance document for incorporating GDEs into sustainability plans (Rohde et al. 2018). This guidance document includes potential approaches and worksheets to identify



Schematic cross section of a riparian groundwater dependent ecosystem associated with an unconfined aquifer to illustrate the effects of groundwater pumping. Graphics by Karley Rodriguez and Amy Merrill.

LEFT: Healthy riparian vegetation in a gaining reach of a stream without pumping, where groundwater is not only supporting the riparian zone, but also supporting higher stream flows in the summer.

RIGHT: Stressed riparian vegetation in the same reach as the left panel due to groundwater pumping. The pumping reduces groundwater elevation and also summer stream flows. As a result, aquatic habitat decreases in quality and extent, and only the largest trees (with the deepest roots) are connected to the local groundwater. Recruitment of younger age classes of riparian trees and shrubs is diminished or ended altogether, leaving far less productive and much more water-stressed vegetation along the channel. This reduces the ecosystem's complexity and productivity, diminishes channel shade, and likely makes the riparian and aquatic corridor habitat far less resilient to disturbance events.

GDEs, assess the effects of groundwater management on GDEs, and develop monitoring networks.

The first step in Rohde et al. (2018) is to identify GDEs within each groundwater basin. To facilitate mapping and analysis of GDEs, the California Department of Water Resources has created a spatial dataset of Natural Communities Commonly Associated with Groundwater (California Department of Water Resources 2018). This map uses existing vegetation maps (VegCamp, CALVEG, and the National Wetland Inventory, among others) to identify areas with (1) wetland features associated with the surface expression of groundwater and (2) phreatophytic vegetation that is generally associated with groundwater. The Natural Communities dataset needs to be locally verified in the field to assess the accuracy of the maps and fill any data gaps. In some groundwater basins GDEs may be identified based on data with a variety of mapping techniques, spatial scale, time period, or level of specificity. Once accurate basin maps are generated, GSAs need to determine the degree to which the mapped ecosystems are connected to groundwater, as phreatophytes can also be tied to an isolated (“perched”) shallow lens of groundwater (not connected to the aquifer used for pumping) or connected to groundwater supplied entirely by local surface waters or agricultural runoff. This requires linking the revised basin GDE map to groundwater elevation data and/or groundwater models compiled by GSAs. Accurately assessing the extent and composition of GDEs is a necessary first step in determining how groundwater management might affect GDEs so that sustainable groundwater targets can be set and a robust monitoring program developed.

There are several challenges in assessing GDEs as part of SGMA. First, little is known about the exchange between groundwater and surface water in many California rivers. This exchange likely varies seasonally and annually according to how much water is available from precipitation and runoff. Spatial variation in groundwater and surface water exchange also occurs due to variable basin hydrology (including tributary inputs) and land use such as water withdrawal. Secondly, because groundwater levels sufficient to support mature trees may not be sufficient to support more shallowly rooted seedlings and saplings (Rood et al. 2003), ecosystem response may vary temporally depending on the frequency and magnitude of disturbance. For instance, groundwater elevations may not be sufficient to support recruitment of pioneer species (such as cottonwoods and willows) needed to

compensate for mortality of mature trees following fires, floods, or senescence. Finally, climate change will likely increase the water requirements and alter disturbance regimes of riparian zones such that maintaining healthy riparian zones may require more groundwater in the future. These uncertainties can be addressed with robust monitoring programs to assess GDE response to groundwater management.

SGMA provides an excellent opportunity to ensure that GDEs are not adversely impacted by groundwater pumping, but requires collaboration between groundwater hydrologists, ecologists, and water managers to ensure its success. Due to uncertainties in the degree to which groundwater conditions will affect GDEs, monitoring programs are required to assess how GDEs adapt to groundwater regimes through time. Ensuring that GDEs are sufficiently addressed in GSPs and monitoring plans will require public participation in GSA meetings by environmentally minded stakeholders.

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ACRONYMS AND DEFINITIONS

GDE - Groundwater dependent ecosystem

SGMA - Sustainable Groundwater Management Act. California law passed in 2014 to ensure groundwater sustainability.

GSA - Groundwater Sustainability Agency. As of August, 2018 there are 264 GSAs for 143 groundwater basins.

GSP - Groundwater Sustainability Plan. Due in 2020 for critically overdrafted basins and 2022 for high and medium priority basins.

Undesirable results under the SGMA: (1) lowering of groundwater levels; (2) reductions in groundwater storage, (3) sea water intrusion, (4) degradation of water quality, (5) ground subsidence, and (6) impacts to beneficial uses of groundwater.



WETLANDS: HOW DO WE PROTECT THEM?

Greg Suba, Julie Neander, & Gordon Leppig

Defining wetlands is surprisingly complicated because numerous state and federal agencies with jurisdiction over them use a variety of definitions and criteria for their delineation (Mitsch and Gosselink 2000). Additionally, the terms used to describe wetlands, such as swamp, mire, bog, marsh, and slough, are often confusing and imprecise.

Simply put, wetlands occur at the interface between terrestrial and fully aquatic habitat. Most wetland definitions include three main criteria: 1) the presence of surface water or a saturated root zone of a sufficient period or frequency to result in the development of, 2) unique wetland (hydric) soil characteristics which are not found in adjacent upland soils, and 3) the prevalence of wetland (hydrophytic) plants adapted to life in saturated soil conditions (Cronk and Fennessy 2001).

Riparian habitats, which in many cases are wetlands, also have a number of competing definitions. Riparian habitats occur adjacent to rivers and streams where

surface and subsurface water connect riparian areas with adjacent uplands and where upland vegetation, in turn, has a significant influence on the aquatic habitat. This riparian influence on rivers and streams includes effects on shade, microclimate, and water temperature. Other riparian habitat influences on streams include bank stability and complexity, off-channel fish habitat, sediment capture, and inputs of large wood and leaf litter. In many areas of California riparian habitat is dominated by willows (*Salix*), cottonwoods (*Populus*), and alders (*Alnus*) but, depending on the region, could also be dominated by numerous other species (see Orr and Merrill this issue).

Since many wetland types can be dry at the surface for much of the year (see Witham et al. this issue), wetland delineations rely heavily on a detailed evaluation of soils and plants. To determine wetland vegetation, plants are placed into five categories based upon their likelihood of occurring in a wetland. These include obligate wetland plants (almost always found in wetlands), to facultative wetland plants (usually found in wetlands) and upland plants (almost never occur in a wetland) (Lichvar et al. 2012). Wetlands can be further classified into categories, such as marine, estuarine, or riverine, and then into narrower habitat types

Above: A stream with an apartment complex built almost on the top of bank. This stream has no room to migrate or for riparian vegetation to provide habitat complexity. The apartment complex is constantly threatened by flooding. Without an appropriate riparian buffer, neither the stream nor people have enough room to safely coexist. Photo by CDFW.

based upon tidal influence, substrate (e.g. rocky shoreline, peat), and vegetation type (e.g. forested, shrub, or grassland) (Federal Geographic Data Committee 2013).

PROTECTING WETLANDS

Both California and the Federal Government have “no net loss” wetland policies. CNPS also has a wetland policy, (cnps.org/conservation/policies). Given the permitting and mitigation costs associated with filling wetlands, it is now much harder to fill wetlands than in years past. Despite this, wetland filling—both permitted and unpermitted—continues to occur. While direct filling is a continuing threat to wetlands, the indirect impacts of development, such as altered hydrology and microclimate, rank with climate change as some of the most pernicious and widespread threats to California’s wetland and riparian habitats (CDFW 2014).

All wetland and riparian habitats are directly hydrologically and ecologically influenced by their upland and upstream environment. This is why the California Rapid Assessment Methodology (CRAM) used by state and federal agencies to assess the habitat quality of wetlands and riparian habitats, takes into account the proximity of adjacent upland native habitat or development. In other words, the quality of a wetland’s ecological integrity is directly influenced by the quality of its adjacent habitat and the quality, quantity, and source of its water supply.

KEY POINTS

- **Land Use Planning.** The most effective protection of wetlands, riparian habitats, and rivers requires a landscape-scale watershed approach. Thus strategic conservation requires effective land use regulations and practices, such as zoning. Without these approaches, commenting on a California Environmental Quality Act (CEQA) document for a project affecting a wetland is a last ditch and often worst case scenario. It is far more effective to have local protections in place guiding development in a more planned and protective manner before a project is proposed.
- **Enforcement is Critical.** Having effective wetland protection regulations on the books will not work if they are not adequately and consistently enforced by local, state, and federal agencies.

- **Monitoring and Management.** Protecting a wetland from development does not mean all other threats disappear. Removing vital disturbance regimes, such as fire, flooding, and grazing can be as much of a threat as altered hydrology and invasive species; all these can substantially degrade a protected wetland. Thus, protecting wetlands means maintaining ecological functions, which typically entails monitoring and active management as well as the resources and staff to accomplish that.
- **Reconnecting Rivers with Floodplains.** For most California rivers, flooding, channel movement (migration), and bank erosion are normal fluvial processes resulting in diverse and complex habitats for fish, wildlife, and plants. For public safety, to protect property, and to allow for farming and development in floodplains, most California rivers have been leveed and thus disconnected from their floodplains. In many cases, bank armoring is considered the only response to bank erosion. This has resulted in a substantial loss of riparian and floodplain habitat. To the extent practicable, local, state, and federal agencies should actively promote safe and feasible opportunities to reconnect rivers to floodplains, restore riparian habitat, avoid bank armoring, and improve open space values for nearby communities.

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WAYS TO CONSERVE WETLANDS AND RIPARIAN HABITAT

Development Setbacks

If it is built too close to a wetland, adjacent development can substantially degrade wetland habitat values. For most wetland types, a development setback of at least 150 feet, and in many cases much more, is needed to prevent direct and indirect impacts of noise and light pollution, domestic cats, invasive species, garbage dumping, and altered hydrology and micro-climate.

Intact Buffers or Greenways

Wetlands are best protected if the development setback is owned and managed by one entity with a conservation objective. A local agency such as a city or county can typically best manage an entire buffer as a park, trail, or greenway. This will mitigate the threats of dumping, erosion, litter, invasive species, etc. The alternative of having every backyard of a subdivision with a piece of the buffer results in "curtilage creep" whereby home owners can develop and utilize their backyard for typical backyard purposes instead of the intended habitat values.

Natural Communities

The vegetation of many wetlands consist of sensitive natural communities with a State Rank of S1-S3. This means impacts to them should be considered during California Environmental Quality Act (CEQA) project review. However many wetland types have yet to have their natural community fully described. CNPS and CDFW are prioritizing describing and mapping of rare wetland natural communities. When commenting on a project affecting wetlands, ensure the natural communities are accurately described, their state status assessed, and potential impacts analyzed.

Cumulative Effects

On-going impacts have led to the loss of a large percentage of various wetland types throughout California. When reviewing proposed projects impacting wetlands, assess if available data on wetland loss could be used to make a fair argument that the project could have cumulative effects, and therefore require mitigation.

California Species of Special Concern (SSC)

Wetlands are often habitat for SSC, including birds, bats, reptiles, and amphibians. Most SSC have undergone range contractions due to significant habitat loss. Many wetland-dependent SSC require adjacent intact upland habitat. When reviewing CEQA projects, ensure the potential impacts to SSC are adequately addressed.

Federal Land Grazing Leases

Wetland and stream impacts from federal grazing leases must be better assessed and minimized. While livestock grazing can be ecologically beneficial and many wetlands benefit from or require a specific disturbance regime, overgrazing is a well-documented threat to wetlands and streams in many national forests, including wilderness areas. When renewing Federal grazing leases, the U.S. Forest Service and Bureau of Land Management should more carefully evaluate the impact of overgrazing on streams and wetlands.

Wetlands in Timberlands

The California Forest Practice Rules (FPRs), which regulate timber harvest activities on private lands, should be strengthened to better protect wetlands from timber harvesting. The FPRs do recognize wetlands, but only "wet areas and wet meadows." Currently there are no standard FPR requirements to prevent timber harvesting in isolated wetlands. The typical protection is excluding heavy equipment from the "wet area."



A stream dominated by red alders (*Alnus rubra*) with plenty of room to flood and migrate and for riparian vegetation to create a complex ecosystem. Photo by Gordon Leppig.

Promoting Beavers

Beavers (*Castor canadensis*) are quintessential ecosystem engineers. In many regions, beaver activities are shown to increase wetland and riparian habitat complexity, prolong summer stream flows, recharge ground water, and hydrate adjacent wetlands and meadows. Where feasible, local, state, and federal agencies should promote the persistence of beavers where their activities are likely to increase habitat values and not substantially conflict with other land uses.

Climate Change Adaptation Planning

Cities and counties should incorporate into their regional plans anticipated climate change effects such as substantial and prolonged droughts; more frequent, severe, and widespread wildfires; and more frequent and greater magnitude floods. If done well, climate change adaptation planning will help protect wetland and riparian habitat while making local communities safer and more climate change resilient.

Sea Level Rise Adaptation Planning

Coastal communities should directly incorporate the most recent and relevant sea level rise, storm surge, and saltwater intrusion scenarios into their regional plans, zoning, and building codes. As many communities rock armor and protect their shorelines, identifying feasible areas for coastal retreat, where estuarine and saltmarsh habitats can migrate landwards, is critical to their persistence.

Resolving Homelessness

In many California urban and suburban areas, people affected by homelessness subsist in makeshift conditions within and on the fringes of wetlands. In many communities this has resulted in significantly degraded wetland and riparian habitat and water quality. This is a complex moral, societal, policy, and environmental issue (and interrelated with addiction, mental illness, and poverty), thus there are many urgent and compelling reasons to meaningfully address this dilemma.

Reporting Water Pollution and Wetland Fill Violations

If you witness what appears to be unpermitted or illegal activity resulting in water pollution, substantial alteration of a stream or lake, or filling of a wetland, you can immediately report it to the California Department of Fish and Wildlife CalTIP Hotline (888) 334-2258; use the California EPA Environmental Complaint System on line form (<https://calepacomplaints.secure.force.com/complaints/>); and contact your local city or county, depending on its location. Be prepared to give a specific location and description of the activity.

REMEMBERING DR. J. R. (BOB) HALLER (1930 – 2016)

Ann Howald, Todd Keeler-Wolf, Bruce Orr,
Diana Hickson, and Michael Barbour

John Robert (Bob) Haller, inspirational teacher, mentor, and renowned California botanist, died peacefully at home, in the presence of his devoted wife and fellow botanist, Dr. Nancy Vivrette, on August 17, 2016. A celebration of Bob's life, including the opening of a display of his magnificent photographs of California landscapes and plants, was held at the Pritzlaff Conservation Center at the Santa Barbara Botanic Garden in December 2016. This tribute summarizes Bob's botanical legacy, with emphasis on his contributions to the understanding of California's rich and complex vegetation, including his role in the formation of CNPS's Vegetation Program.

Bob Haller was a revered and much-beloved instructor and mentor to the hundreds of University of California, Santa Barbara (UCSB) students who took his most famous course, Plants of California, Botany 103. Bob inspired so many through his sheer love for the beauty and diversity of California landscapes and plants, which he introduced to us through his rigorous teaching, his gentle manner, and his captivating photographs. Class field trips with Bob were truly awe-inspiring—long days immersed in iconic California landscapes, learning to recognize the dominant species of each plant community (as we called them then), and keying plants from dawn till dusk. As one former student said, “Bob ... quietly and unassumingly led us on an amazing journey of discovery. I owe him a great debt of gratitude and look back on the experience with considerable joy.”

Dr. Haller also was a renowned researcher on California pines, especially *Pinus jeffreyi* and *Pinus ponderosa*, work he began in 1951 while at UCLA, studying under Dr. Harlan Lewis, and Dr. Mildred Mathias. He would continue studies of Jeffrey and ponderosa pines throughout his professional career. Bob's well-documented research collection of pine voucher specimens, The John Robert Haller Pine Collection, which comprises approximately 5,000 specimens from 300 different localities, is housed at the Cheadle Center for Biodiversity and Ecological Restoration (UCSB) where it provides a resource for genetic and phenotypic variation (Carroll 2011).

Bob recognized the multi-layered complexity of California's native vegetation and sought a way to



Bob Haller on a SBBG field trip to a lake basin in Plumas County with Cathy Rose, Avis Keedy and Chris Walden. Courtesy of the Santa Barbara Botanic Garden.

organize and describe that complexity. This led Bob to develop his own framework for classifying California vegetation, which each of his students committed to memory, and which then provided the foundation for the Cheatham and Haller (1975) Annotated List of California Habitat Types (see sidebar) that was developed as a resource for management and future acquisitions of the recently established University of California Natural Land and Water Reserves System (NLWRS, now the UC Natural Reserve System or NRS). During the 1970s and early 1980s, Bob served as the Faculty Manager for several reserves that were managed by UCSB, and he was instrumental in the addition of Valentine Camp and the Sierra Nevada Aquatic Research Laboratory, today known together as the Valentine Eastern Sierra Reserve, to the NLWRS.

After his retirement from UCSB, Bob continued his research on pines, was an active participant in the CNPS Vegetation Committee, and began a second career as the education botanist at the Santa Barbara Botanic Garden. With his wife and colleague Nancy Vivrette, and his co-worker Mary Carroll, Bob led field trips throughout California, the Western U.S., and even far-flung corners of the globe, thus introducing new generations, young and old, to fields of flowers, conifers big and small, and endless other botanical wonders.

DEFINING HABITAT TYPES

As a young UCSB associate professor, Bob Haller along with colleague Dan Cheatham (a field representative with the newly-formed University of California Natural Land and Water Reserves System), were asked to develop a classification to guide the NLWRS in establishing scientific reserves encompassing all of the major habitats throughout California. Bob and Dan's endeavor was simultaneous with the publication of the seminal *Terrestrial Vegetation of California* (Barbour and Major 1977). The book was originally intended to have four additional chapters, one of which was a compendium of habitat types of the state developed by Cheatham and Haller. Unfortunately space and cost precluded their addition and the Cheatham and Haller classification system, which included approximately 200 habitat types, was never published. However, the 1975 draft manuscript of the chapter (Annotated List of California Habitat Types) still became widely used, thanks to the authors' generosity. Today we realize it was the organizational foundation for understanding California's vegetation. The Cheatham and Haller clas-

sification was based on Bob Haller's vast knowledge of California, which incorporated botany, climatology, geology, geography, and plant evolutionary history.

Even to those who never saw the original manuscript there is something familiar about the organization of habitat types to most of us who have been interested in California's natural history.

Holland's version of the classification, used as the state standard for natural communities between 1986 and 1995, was a direct descendant of the well-organized catalog of Cheatham and Haller, even down to the basic numbering system. Moreover, 23 years after the circulation of Holland (1986), and following the addition of a vast quantitative databank of vegetation sample plots, one can look into Appendix 3 of *A Manual of California Vegetation* (Sawyer et al. 2009) and note the similarities in hierarchical structure of basic levels of the state classification:

Vancouverian Coastal Dune and Bluff

- Vancouverian/Pacific dune mat
- California Coastal evergreen bluff and dune scrub
- California-Vancouverian semi-natural littoral scrub and herb vegetation

California Coastal Scrub

- Central and South Coastal Californian coastal sage scrub
- Central and South Coastal California seral scrub
- Naturalized non-native Mediterranean scrub
- Coastal Baja California Norte maritime succulent scrub

Although we have added much more detail, the organizing concepts of vegetation Bob and Dan used back in the early to mid-1970's have been largely retained. Despite years more effort demonstrating the finer points of floristic relationships we still see broad patterns of vegetation in a similar way to Cheatham and Haller's; truly a testament to their deep knowledge and timeless understanding (a digital copy of the Cheatham and Haller December 1975 manuscript can be obtained by contacting author Keeler-Wolf - Todd.Keeler-Wolf@wildlife.ca.gov).

```
3.0 SCRUB AND CHAPARRAL
  3.1 Coastal Bluff Scrub
    3.11 Northern Coastal Bluff Scrub
    3.12 Southern Coastal Bluff Scrub
  3.2 Coastal Scrub
    3.21 Northern Coastal Scrub
    3.22 Central Coastal Scrub
    3.23 Coastal Sage Scrub
    3.24 Maritime Cactus Scrub (also listed as 3.51)
    3.25 Coastal Dune Scrub (also listed as 2.22)
```

Excerpt of the classification for California Scrub and Chaparral from the original Cheatham and Haller (1975).

```
30000 SCRUB AND CHAPARRAL
  31000 Coastal Bluff Scrub
    31100* Northern Coastal Bluff Scrub
    31200* Southern Coastal Bluff Scrub
  32000 Coastal Scrub
    32100 Northern (Franciscan) Coastal Scrub
    32110 Northern Coyote Bush Scrub
    32120 Northern salal Scrub
    32130 Northern Silk-tassel Scrub
    32200 Central (Lucian) Coastal Scrub
    32300 Venturan Coastal Sage Scrub
```

Same excerpt from the widely-known Holland (1986) list of California Natural Communities.

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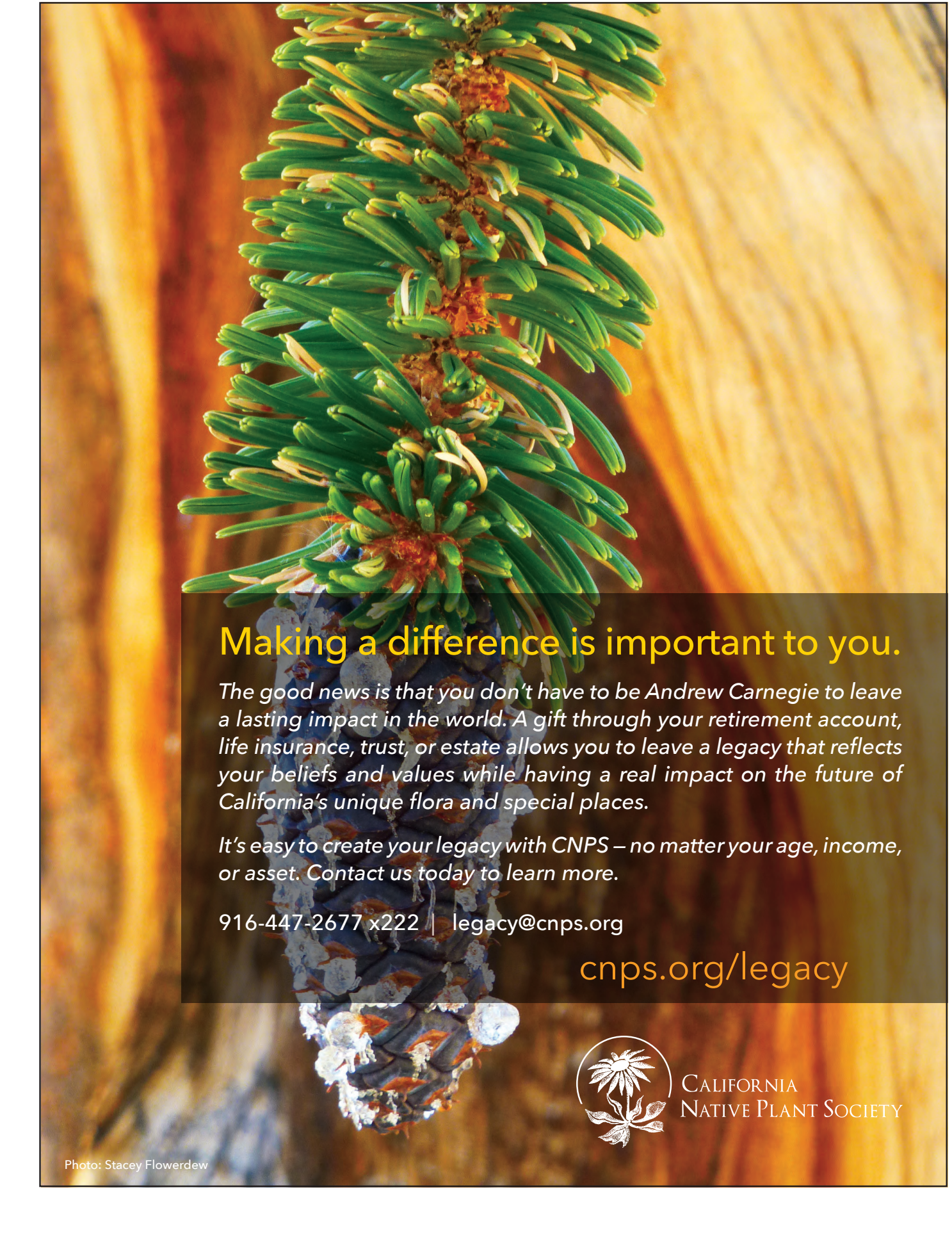
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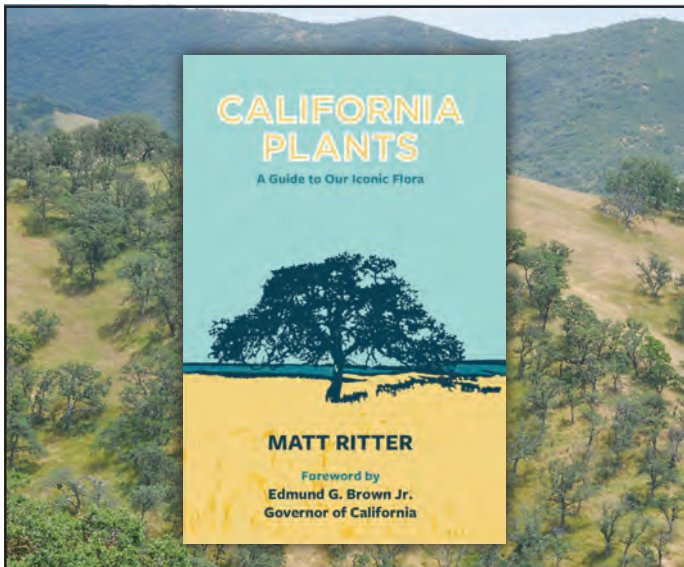
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Foreword by California Governor **Jerry Brown**

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Isinglass Lake in the Marble Mountain Wilderness. INSET: English sundew (*Drosera anglica*). Photos by Michael Kauffmann.

From the Editor

Trampolining. I recently had a new experience on a wetland in the Marble Mountain Wilderness when I was searching for the only documented population of English sundew (*Drosera anglica*) in the Klamath Mountains. When I approached the lake the ground began to move—bubbles emerged around my feet and several feet away at the lake's edge. I quickly took a few steps backwards.

This was my first experience walking on a peat bog and I will never forget the magic of the moment. What

made the biggest impression on me was how long this bog, and the peat itself, took to form.

The same can be said for any great organization with a history of conservation and botanical story telling. I am honored to have spent several years as *Fremontia* editor and contributed to that history. This issue will be my last, but into the future I look forward to finding it in my mailbox and reading it, cover to cover, with all the edits and layout finalized!

- Michael Kauffmann, www.michaelkauffmann.net



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